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The Early European Potato: its character and place of origin. By **Redcliffe N. Salaman**, F.R.S.

(With a map and 25 figures in the text)

[Read 11 May 1944]

Fifteen years ago, the first part of our task could have been dismissed by a few references to Clusius, Gerard, and their brother herbalists; and for the latter, its original home, to a discussion inconclusive, it is true, because of lack of evidence if based on history, and of material if on taxonomy, between the upholders of a Chilean, as opposed to those of a Peruvian origin. To-day, the problem is both simpler and more complex. Simpler because we have much more data on which to form an opinion, and more complex because we have come to realize that the potato is a plant with a long and varied past and that many quite distinct species were brought into cultivation by the early inhabitants of South America.

Our new knowledge of the potato is derived in the main from the work of the Russian botanists who, under Vavilov and his colleagues Bukasov, Juzepczuk and others, made an exhaustive study of the tuber-bearing Solanums of Central and South America between 1926 and 1932.

They discovered and described a large number of species whose somatic chromosome formulae ranged from $2n=24$, $2n=36$, $2n=48$, $2n=60$, to $2n=72$. The only group, however, which concerns the problem under consideration, is that possessed of the chromosome equipment $2n=48$, for it is to this alone that the European domestic potato belongs.

As a result of these expeditions, and a study of the extensive material they brought back with them, Bukasov and his colleagues convinced themselves that there were two main centres of species differentiation for the $2n=48$ group of potatoes: the one with its centre in the high Andes in the neighbourhood of Lake Titicaca, and the other in the Island of Chiloé and the nearby coastland of Southern Chile. The two regions are quite distinct and are separated by the desert of Atacama and a high chain of mountains covered with perpetual snow. They further concluded that from these two centres two quite distinct species of potatoes had evolved, and that in both regions they had been from an early date brought into cultivation. The Andean potato of the $2n=48$ formula they called *Solanum andigenum*, and that from Chiloé, *S. tuberosum*.

The choice of the latter name was based on the consideration that there was, in their opinion, a very close resemblance between the types of cultivated potatoes growing in the Chiloé district and those in general use in Europe, to which, of course, this name, *S. tuberosum*, had been applied ever since the time of Gaspard Bauhin (1596), whilst such resemblance was not apparent between the latter and Central Andean forms.

Bukasov writes: 'From the mountainous center in the Andes, the Chiloéan center on the south coast, where *S. tuberosum sens. str.*, the ancestor of all our commercial varieties, took its origin, must be separated.' And again: 'It may be doubted whether *S. tuberosum* is adapted to the conditions prevailing in the Andes and whether it is able to compete there with the Andean species. Otherwise, what could explain the fact that among hundreds of examples of indigenous potatoes in Colombia, Peru and Bolivia, not a single example of *S. tuberosum* occurred.' And in support of this thesis, he hazards the following: 'There is no doubt that the number of immigrants who brought with them *S. tuberosum* from Europe was not a small one in these Andean countries. Possibly the Andean species are ecologically incompatible with *S. tuberosum*' (Bukasov, 1930), implying, of course, that such introductions of the European potato had been tried many times, and that they had failed to hold their own. Whilst there is no evidence of such having occurred, their failure would be no proof of the truth of the generalization suggested.

Prof. Juzepczuk, in a personal letter dated 17 March 1936, goes even further when he states that 'Many facts and notions confirm our supposition that the complexes of forms designed by us as *S. tuberosum* and *S. andigenum* originated quite independently one from the other from absolutely distinct wild forms and were introduced into cultivation by widely different peoples'.

Finally, Bukasov rules out *S. andigenum* as the possible original of the European potato, on the following grounds: 'The specific composition of the Colombian potatoes and the conditions of transport in Colombia, which four hundred years ago were much more primitive than they are now, categorically rule out the version of the original introduction of the potato into Europe from the Capital of Colombia, Santa Fé de Bogotá, as well as from the Venezuelan port Santa Fé' (Bukasov, 1930).

The distinguishing characteristics of the two species *S. andigenum* and *S. tuberosum*, to which we shall refer later, are set out by Bukasov in a further publication, but here it should be noted that although he derives our domestic potato from Chiloé, he insists on the necessity of distinguishing between the existing European group of *S. tuberosum*, for which he suggests the group appellation *S. tuberosum* var. *europaeum*, and the original Chilean *S. tuberosum*, from which he holds they were derived. In what manner these two latter groups differ, other than in the greater range of variation common to the former and in the absence of deep purple-flowered variations,[1] is not stated.

Bukasov describes two wild Chilean species of the chromosome formula $2n=48$, viz. *S. Molinae* Juz, and *S. leptostigma*. It is this latter which he believes to be the original parent of the Chilean domesticated group of which he describes thirty-one distinct varieties.

In 1935 (Bukasov and Lechnovitz, 1935), and in 1936 and 1937, Bukasov again emphasizes the distinction between the two species *S. andigenum* and *S. tuberosum*, and the advantages to be gained by their interbreeding.

Some have thought to find support for a Chiloéan origin of our domestic potato in the remarks of that very accurate and distinguished authority on the history of the potato, Roze: that they have misunderstood him is obvious from the following translation of the relevant passage: 'According to the facts as ascertained by naturalists and explorers, one may be permitted to conclude that the origin of the wild potato should be assigned to the mountainous district situated between Chile and Araucania.' This may be regarded as being the district around Concepcion, lat. S. 37°, some 450 miles north of Chiloé and in the region assigned by Bukasov to the *S. tuberosum* species. But Roze does not suggest for a moment that it was thence that the potato was introduced to Europe, but that it may have been from hereabout that it spread through South America. He continues: 'It was first cultivated in Chile itself, then in Peru where the Incas did much to extend its cultivation on a large scale....There is no historical or documentary evidence which makes any mention of the introduction of the potato into Spain. It reached Spain without doubt, by accident, probably as a residue of the food stores on the ships carrying treasure back to Charles the Fifth' (Roze, 1898). Berthault (1911), who is also claimed as a supporter of the Chilean origin, merely quotes the words of Roze recorded above, without comment.

The treasure, whether that which was looted from the Incas, or that won from the mines of Potosi in Bolivia, was invariably exported from Callao, the harbour of Lima, nearly two thousand miles to the north of Chiloé which, in point of fact, had not even been sighted till 1559, three years after Charles abdicated.

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[1] Deep bluish purple flowers do occur amongst our cultivated European stocks, e.g. 'Surprise', 'Eightyfold' and 'Catriona'.

Vesselowski (1934) does not share his colleague's opinion; he writes: 'The potatoes of the Andes constitute a very large species possessed of an extremely large number of characters, viz. *S. andigenum*, of which the European potato *S. tuberosum* represents one sub-species, characterized by a much more limited range of characters'; a view which the writer reached independently and which was explained and defended in the Masters Lecture (Salaman, 1937).

Bukasov, nevertheless, has adhered to his views on the origin of the European potato, although he admits that in Chiloé and neighbourhood, the only varieties which could definitely be said to belong to the domestic group as we know it in Europe, were almost certainly 'escapes' from Europe, viz. 'Up-to-date' and 'Early Rose', and that there are differences which are not defined, between the native cultivated potatoes of those parts and our own domestic potato.

The views of the collector and botanist, Wight (1910), who travelled widely in S. America and had an intimate knowledge of the literature and herbarium material, are of interest in this connexion. Writing in 1910, after a recent visit to Peru and Chile, he says that he failed to find any wild potato in Chile other than *S. Maglia*, and that there were far greater differences between the various cultivated varieties of Bolivia and Peru than amongst those growing in Chile. This led him to regard the former as the original centre of distribution. Wight, impressed by the fact that the Isle of Chiloé and the neighbouring mainland are rich, well-wooded regions capable of harbouring a considerable head of game, suggested that the early settlers would have adopted a nomadic hunting culture, whereas those who made the Andean altiplano their home, were forced to adopt an intensive cultivation of the soil, in which the potato played an important part. Hence it is to be presumed that the domestication of the potato took place first in Peru and Bolivia, and spread from thence both to the north and the south. The wide diffusion of the common native name 'papa', a Quichuan word for the potato, gives additional force to the argument.

Later he wrote that: 'There is no botanical evidence that the species [to which the domestic potato is ascribed] is now growing in its original indigenous condition anywhere. So far as the number and relationship of the species referred to the section *Tuberarium* are concerned, the evidence is in favour of the Central Andean region' (Wight, 1917).

Below are set out the distinguishing features between *Solanum andigenum* forms, and our domestic potato *S. tuberosum*, according to statements to be found in Bukasov's publications of 1930, 1933, 1936, and in a letter dated 17 March, 1936, to the writer, which he has kindly permitted me to make use of. Sentences contained in square brackets are comments contributed by the writer.

Stems. In *S. andigenum* are usually longer; the internodes, especially the lower ones, longer. [The stems are thinner in typical *S. andigenum*, and the plants generally tend to sprawl.]

Leaves. In *S. andigenum* the leaves are widely spaced on the stem and are set at an acute angle with it. In *S. tuberosum* the leaves are more densely disposed and are set nearer to a right angle with the stem. In *S. andigenum* the leaves are strongly dissected [i.e. numerous secondary and often tertiary leaflets are present, but this is very far from being general].

Leaf segments. Are smaller in *S. andigenum*. In *S. tuberosum* they are usually broad; in *S. andigenum*, generally narrower.

Rachis. In *S. andigenum* is generally upright [straight]; in *S. tuberosum* generally arched.

Pedicels. In *S. andigenum* generally abruptly narrowed at the base of the calyx; in *S. tuberosum* they pass gradually into the calyx base.

Hairs on the flower. In *S. tuberosum* they are longer and more bristle-like; in *S. andigenum* shorter and less stiff.

Calyx. In *S. tuberosum* they are large, with well-developed, sharp ends to their sepals, which are almost of uniform size, and symmetrically disposed. In *S. andigenum* they are not so large: the sepals have shorter, sharp mucrons, sometimes not uniform in size, and usually not symmetrically disposed. [The sepals in *S. tuberosum* are almost always furnished with mucrons of unequal size.]

Corolla. Intensive purples common in *S. andigenum*; they are rarer in *S. tuberosum.*

Anthers. In *S. tuberosum* they are often not fully developed, and, if well developed, are long. In *S. andigenum* they are well developed and generally shorter, and always perfect.

Stamen filaments. In *S. andigenum* they are thinner and rarely yellow. In *S. tuberosum* they are very thick, generally about 1·5 mm. across.

Stigma. In *S. tuberosum* it is very large. In *S. andigenum* it is smaller.

Style. In *S. andigenum* is thinner and not twisted. The papillae at the basal end of the style vary in length according to the variety. [These structures in *S. andigenum* are not referred to in the differential diagnosis in either the 1930 or 1936 communications.]

Berries. In *S. andigenum* they are freely formed.

Seeds (according to Perlova). In *S. tuberosum* they are for the most part pubescent; the projection slightly pointed, or somewhat blunt. A characteristic feature is that around the projection there is a light membranous border. The seeds have a smooth surface. Size 2·1 × 1·1 mm. Index 1·9. In *S. andigenum*, seeds are pubescent, surface not smooth, slightly wrinkled. The membranous border round the projection is absent. Size 2·0 × 1·1 mm. Index 1·8.

Tubers. In *S. tuberosum* they form in a long-day environment; in *S. andigenum*, in a short-day one.

Physiological characters. *S. andigenum* varieties are more resistant to attack by *Phytophthora infestans* than those of *S. tuberosum.* [No evidence of such resistance has been found by the author.]

Formation of tubers. This occurs much later in *S. andigenum* than in *S. tuberosum.*

Resting period of tubers. Longer in *S. andigenum* than in commercial varieties.

In assessing the diagnostic value of these differentia, it must be remembered that the Russian authors have always admitted that there is a considerable range of variation in the characters to be found in the collective species of *S. andigenum*; and all are agreed that the group of potatoes cultivated in Europe which are here referred to as *S. tuberosum* are notoriously variable. Hence the comparison must be regarded as being between the most representative forms of the two species. Bukasov accounts for the wide range of variation seen in our domestic potatoes by the number of different parental stocks which he assumes came to Europe from America in the sixteenth century, and to such others as have been added during the centuries.

By a close comparison of the early descriptions of the potato, see Table 1 (p. 5), an attempt has been made to determine how many different varieties were described in Europe in the fifty or sixty years following the receipt by Clusius of his potato in 1588. It would appear that there were not more than four, three of which may conceivably represent original importations, though the possibility of one or other being a seedling bred in Europe cannot be lightly dismissed.

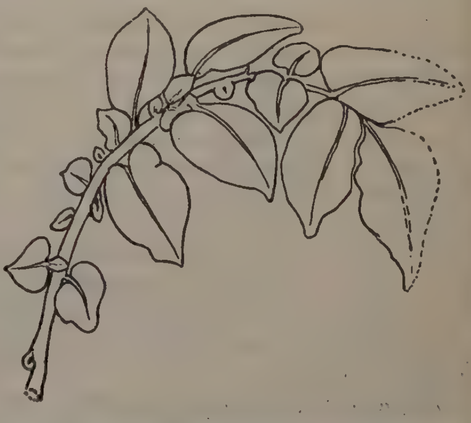

Fig. 1. A leaf from the reproduction of the aquarelle made in 1559 of the plant grown from tubers sent to Clusius by Philippe de Sivry, 26 Jan. 1588. From the Frontispiece to Roze's *Histoire de la Pomme de Terre.*

TABLE 1

Author and date of publication	Habit of haulm	Length of stem	Division of leaf	Secondary leaflets	Colour of flower	Shape of tuber	Colour of tuber	Number of tubers	Maturity	Variety
Gerard, 1597	Sprawling	—	Compared with parsnip	Probably present	Heliotrope	Round to oval; knobbly	Brown, i.e. a dirty white	Many	Main crop	'A'
G. Bauhin, 1596	Vigorous, sprawling	Usually 2–3 ft., may be 5–6 ft.	Six or eight primary leaflets, of which one is terminal	Regularly placed between the leaflets, one-sixth the size	Bluish purple, anthers reddish	Irregular, round, knobbly	Brown or reddish black	—	Late	'B'
M. Chmielecius, 1596	Like a spreading shrub	—	—	—	White	No tubers	—	—	A very late seedling	—
O. de Serres, 1600	Sprawling	5–6 ft.	—	—	White	—	Light brown	—	Late	'C'
C. Clusius, 1601	Sprawling	6–7 ft.	Five to seven, one being terminal	Present between the primaries	'Pale purplish', ? heliotrope	Variable, knobbly	Reddish purple	40–50	Late	'D'
J. Hogeland, 1601	—	—	—	—	White	No tubers	—	—	A very late seedling	—
G. Bauhin, 1620	Bushy and sprawling	2 ft. 8 in. to 4 ft., sometimes to 6 ft.	Six to eight, plus one terminal	A pair between each pair of leaflets	Blue or purple with reddish yellow anthers	Very irregular, knobbly	Black or red	40–50	Late	'B' and 'D'
J. Parkinson, 1629	Sprawling	—	Many primary leaflets	Secondaries probably present	Pale bluish purple, dove colour, ? heliotrope	Irregular, knobbly	Light brown	—	—	'A'
R. Dodoens, 1644	Thick	8 ft. or more	Two or three pairs and terminal	Present	Purple upper-surface, whitish under-surface	Small, up to 2 oz. in weight	Red or purple, sometimes purple inside	50 or more	Very late	'D'
J. Bauhin, 1651	—	3 ft. to 4 ft. 6 in. and more	Three pairs	Second and ? tertiary present	Pale to purple, some white	Large, irregular	Black to red	—	—	'B'

However that may be, the range of characters these four display would, by their inbreeding, provide an ample basis for all the subsequent variations which have appeared amongst our domestic stocks.

Our European stocks have been reinforced in the last hundred years by the importation of a very few new parents from South America, two only of which are recorded, viz. Daber's potato in *circa* 1830, and Goodrich's 'Purple Chile' in 1849. Of the first we know little: it is generally presumed to have come from the north of South America, and hence would have been a variety of *S. andigenum*; the second was acquired in Panama, and was, without doubt, an *S. andigenum* variety. The name given to it by Goodrich has misled Bukasov, as it did at one time the writer (Salaman, 1926), into imagining that the large progeny to which it has given rise through its grandchild, 'Early Rose', were, in a sense, reinforced members of the Chilean *S. tuberosum* species. That is not the case.

Notwithstanding the justifiable prestige which attaches to the names of the Russian scientists who have described the distinguishing characters of the two groups, it is necessary to consider whether all the differentia mentioned have an adequate validity for this purpose, and, still more, whether one is justified in using them as guides towards the solution of our problem, the origin of the domestic potato. It is not difficult to eliminate those which, in the writer's opinion, entirely fail to substantiate their claim in either of these capacities. And here it should be remembered that one is using the term *S. tuberosum* as applying to our domestic series, and *S. andigenum* to those varieties emanating from the Lake Titicaca region northwards and southwards into the northern Argentine.

(1) *Pedicels.* The question whether the passage of pedicels into the calyx is sudden or gradual, is found to be extremely difficult to appreciate, and very uncertain in its incidence.

(2) and (3) *Hairs on the petals, and the size of the calices.* The differences noted are neither sufficiently evident nor constant to be of value.

(4) *Anthers.* The alleged distinctions are as often wanting, as present. Very many domestic varieties have perfect anthers, though it often happens that they are larger than those of the average *S. andigenum*, and are relatively broader.

(5) *Stigma.* The size and shape of this structure in *S. tuberosum* is so variable as to render it useless as a differential character. It is frequently as fine as in any of the *S. andigenum* varieties.

(6) *Seed.* The writer has been entirely unable to confirm any of the differentia mentioned. In particular, the seed of all the typical *S. andigenum* specimens examined were found to be furnished with exactly the same development of membranous border as are those of the domestic varieties, and as were the two Chilean *S. tuberosum* varieties examined.

(7) *Berries.* Are formed on many of the domestic varieties in possibly greater excess than is to be found on those of *S. andigenum*, e.g. 'Myatt's Ashleaf', 'Flourball', and 'Katie Glover'.

(8) *Resistance to* Phytophthora infestans. No resistance to either of the strains 'A' or 'B' of this fungus was found in any of the forty-six varieties of *S. andigenum* examined for the writer by his colleague Mr M. Pettersson at Cambridge, for this quality. Nor, indeed, is it to be found in any of our domestic potatoes now in use; nor is it known in domestic stocks, except for the few immune and resistant varieties not yet issued to the public, which have been raised by the writer and others from *S. demissum* crosses.

Before we consider what validity is to be attached to the remaining differentia, it is necessary to review the type of potato plants which are, by common consent, included under the banner of *S. andigenum*.

It may be said at once that there are a large number of varieties growing in the area of South America extending from Titicaca and the Jujuy province of Argentina in the south, to Cartagena in the north, whose characters fall readily into a single group picture coinciding in a large measure with that drawn by Bukasov.

Such plants, by reason of their many long, thin stems; upward pointing leaves; small, narrow, widely spaced leaflets; small and only occasionally numerous secondary leaflets; their open[1] as opposed to closed leaf; their abundant and commonly bluish-purple flowers, and very late-maturing tubers, are at once marked out as being distinct from the great majority of European domestic potato plants. The type described may be regarded as representing the commonest form of the *S. andigenum* species growing in the Central Peru-Bolivia areas. But to the north and south of this area, in Ecuador and Colombia on the one hand, and the province of Jujuy in North Argentina on the other, other types are to be found, all of which are included by the Russian writers in the collective species of *S. andigenum*, although they differ very materially from the above, and approximate in varying degree to our European varieties as will be shown later.

Of the differentiating characters which have been set out, one allows of actual measurement, viz. the width of the staminal filament, and another to a more or less exact representation, viz. the character of the leaf and its constituent parts. To the consideration of these we must now turn.

Bukasov (1933) gives measurements of the diameter of the anther filaments in a few of the varieties of *S. andigenum* of Central and South Peru and Bolivia, as well as of those of several Chilean varieties, but unfortunately only one of the varieties which occur in the northern, and none from the southern extremities of the *S. andigenum* area. The measurements shown in the two tables on p. 8 are abstracted from Bukasov.

The two sets of contrasting measurements give an average width of filament of 0·98 mm. for the *S. andigenum* group, and 1·09 mm. for that of the *S. tuberosum* of Chiloé. A difference which amounts to but 10 % of the higher figure would not seem to have any great significance, seeing that there are very considerable variations recorded in some cases for a single variety. But be that as it may, such value as these figures might appear to have, vanishes in face of the following remark, which occurs in the same communication: ‘With regard to the other flower characters, the commercial varieties in general are clearly delimited from the second group of *S. andigenum* for which thicker filaments are known, from the Central Peruvian and Colombian forms in which the filaments reach on an average 1·37 mm. but not up to 1·5 mm. as in the Chilean form, or 1·79 as in the commercial varieties’ (p. 181).

The other group of *S. andigenum* referred to is that of Bolivia and South Peru ‘where they [the filament widths] reach only by way of exception the lower limit of thickness known for “Up-to-date” [an English variety], i.e. 1·15 mm.’

Of European varieties, the Russian author found but two in cultivation in South America, viz. ‘Up-to-date’ and ‘Early Rose’, whose filaments varied in width from 1·15 to 1·3 mm.

When one remembers that ‘Early Rose’ is the grandchild by selfing of an *S. andigenum*

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[1] Leaves are spoken of as being ‘closed’ when the development and disposition of both the primary leaflets, and the secondaries when present, is such as to fill up the whole, occluding more or less completely any free spaces between the leaflets. An ‘open leaf’, on the contrary, is one in which such a development has not taken place and, in consequence, considerable open spaces exist between the leaflets. Intermediate forms are common. The difference between the types of leaves is shown in Figs. 18, 22 and 24 representing the open, and Figs. 14, 19 and 21 the closed type; and Figs. 20 and 23 the intermediate form. In our own potato fields, a comparison of the respective leaves of ‘King Edward’ and ‘Sharpe’s Express’ will demonstrate the distinction between the open and the closed types, whilst in ‘Majestic’ and ‘Kerr’s Pink’ will be found good examples of the intermediate form. The outlined tracings are in all cases drawings from preserved leaves, except in the case of Fig. 1.

Width of anther filaments in varieties of S. andigenum

	Average thickness mm.
Bolivia var. *bolivianum* form *arcuatum*	1·0
South Peru var. 'Ckello huaccoto' form 'competillo'	1·0
said to be thick, therefore more than	1·0
var. *Sihuanum* 1·0 m. below and 0·8 m. above	0·9
var. *Herrerae* 'not thick'	1·0
Central Peru. Subspecies *tarmense* (the flower is exceptionally small)	0·85
Colombia. From 1·0 to 1·27 m.	1·13
Average width	0·98

Width of anther filaments in varieties of S. tuberosum *sens. str.*

	Average thickness mm.
Chiloé var. *chilotanum*, 'from 0·7 to 1·0'	0·85
var. *chilotanum* form shaped, same as above	0·85
var. *chilotanum* form *thalassinum*, 'from 0·95 to 1·020'	0·99
var. *chilotanum* form *monticum*, 'from 0·9 to 1·200'	1·05
var. *elegans*, 'from 1·0 to 1·120' occasionally up to 1·2	1·06
var. *villaroella*, 'from 0·9 to 1·250'	1·07
var. *recurvatum*, 'from 1·100 to 1·350'	1·22
Chiloé varieties of the leptostyla group	
var. *multibaccatum* form *elongatum*, 'from 0·8 to 1·050'	0·92
var. *multibaccatum* form *brevipilosum*, 'from 1·2 to 1·35'	1·27
var. *crassipedicellatum*, 'from 1·1 to 1·150'	1·12
var. *yutuense* form *infectum*, 'up to 1·5 m.'	say 1·25
var. *crassifilamentum*, 'up to 1·80, the thickest in *S. tuberosum*'	say 1·5
Average	1·09

variety from somewhere near Panama, probably Colombia, we may be permitted to draw three conclusions:

(*a*) That Bukasov's measurements must not be taken too seriously, because neither the number of measurements nor the range of variation is given; nor, as we have seen, are the individual measurements consistent with the general statement made later in the same paper, as to the average measurements in the two groups.

(*b*) That in general the Chiloéan *S. tuberosum* varieties may have thicker filaments than the *S. andigenum* varieties of Bolivia-Peru.

(*c*) That some, at least, of the Colombian *S. andigenum* are possessed of filaments considerably broader than those to be found in the *S. andigenum* forms growing in the centre of the area of distribution, and that these filaments may be as broad as those in some of our domestic varieties.

It is this last conclusion which has some bearing on the problem of the provenance of our European potato.

When we turn to the form of leaf and habit of the plants, we are, especially as regards the former, on more secure ground. It is for this reason that the writer has preserved adult leaves from plants of the South American varieties of the European Collection growing in the open under the direction of Dr J. G. Hawkes. He has also to thank him for allowing free access to his herbarium collection, for permission to make tracings of leaves from the specimens there preserved, and for information as to the character of the growing plants. In addition, the writer has been able to compare all the above with his own collection of preserved leaves of European domestic varieties, and of seedlings bred from these.

An examination of this material has allowed of the division of the highly representative collection of *S. andigenum* material into a number of groups, the characters of which are set out below. It must be borne in mind that we are dealing with material which does not lend itself to very exact measurements or precise definition. Variations of a minor character, such as occur between leaves occupying different positions on the main stem, have been overcome to a large extent by the selection of fully adult leaves, usually from the third node above ground. Other variations may be seasonal; others are secondary to the soil conditions and their consequent effect on the rapidity of growth, but such do not affect the fundamental character of the leaf. An experienced observer looking at the tracings will, it is hoped, have no difficulty in recognizing the distinctive character of the norm of each group, as well as the gradual passage of one into the next.

The Cambridge material was collected by Dr Hawkes and his colleagues from the areas set out below. Of some, only tubers were obtainable, and such have been grown in Cambridge and their leaves preserved by the writer, but for most the growing plants were preserved at the time of collection as herbarium specimens and their tubers were sent to England. No attempt was made to select any particular type of plant; on the contrary, all available domesticated varieties were sought for and accepted. The collection consists of 139 cultivated varieties culled from most of the principal potato-growing areas throughout the distribution area of *S. andigenum* as delineated by Bukasov, and shown in the map on p. 10.

In a few instances, material grown at Cambridge has been self-fertilized, and some of the seedlings are included under the regions from which the parents were derived. There are thirteen in all, and they are fairly evenly distributed throughout the various areas.

Before describing the various groups, a word must be said as to the rationale and the method of classification. In the first place, the whole material, consisting of more than 250 examples of the 139 distinct varieties, for often there were several specimens of a single variety preserved, were grouped into classes, without any reference to their place of origin. It was at once apparent that those varieties which are furnished with small and simple leaves, and which have been placed in Group I, could be at once distinguished from those large broad-leaved types with wide leaflets which have been ascribed to Groups V and VI. With these two main types out of the way, the remainder were examined for the occurrence of other distinguishing characters: this led to the construction of Group III, whose members, by reason of their elongated leaf and unusually long petiolule, formed another consistent class.

Group II consists of those varieties whose leaves are of the same general character as that of Group I, but in which the leaf is bigger, the leaflets broader, and the development of secondary leaflets greater.

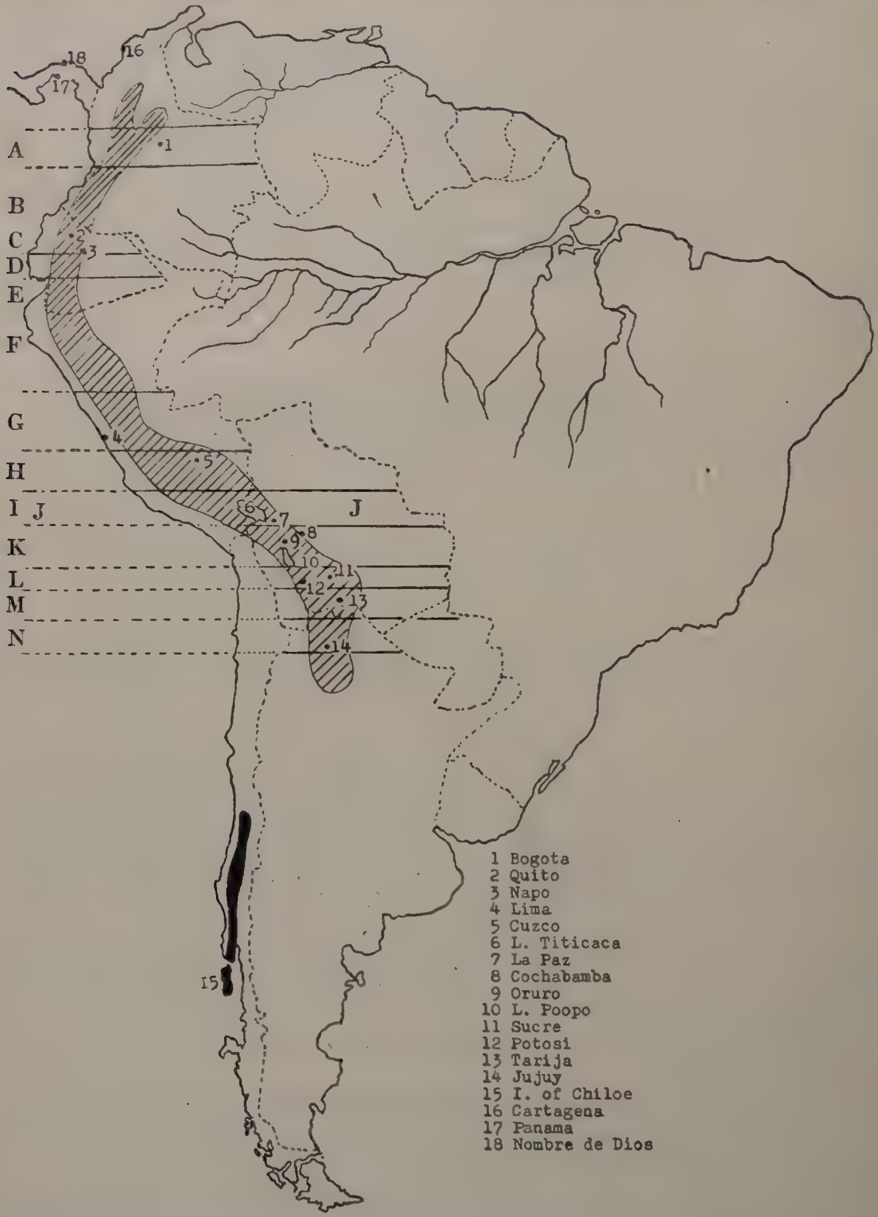
Group IV was made up of those varieties, the character of whose leaves was intermediate between Groups III and V.

Groups V and VI, as far as leaf characters are concerned, are scarcely to be distinguished, the distinction between the two lying in the fact that the haulms of Group VI are more or less typical of the European varieties, whilst those of Group V are more akin to those associated with the *S. andigenum* types. Thus the whole trend of the classification is the passage from the more simple to the more developed and specialized type of leaf, from the typical *S. andigenum* to that of the cultivated variety of Europe.

Reviewing the material thus subdivided into five groups, Groups V and VI being regarded as one, it was apparent that the leaf characters of the varieties within each varied around a norm in such a manner that, whilst it was easy to recognize the distinctive features of the successive norms, a gradual confluence of characters could be observed between the less conforming members of any two successive groups.

In Table 2 is set out the localities from which the varieties originate, with their map reference, their respective grades, and their distinctive numbers within the collection.

Group I. The leaves are small: 3–6 in. long, the leaflets are sharply pointed and relatively narrow; the first pair are set at an acute angle with the rachis, and the subsequent ones at angles of about 75°. (In the tracings, this latter feature is sometimes obscured by a displacement which has taken place at the time of preserving.) Four pairs of primary leaflets is the rule, a fifth or sixth pair not uncommon. The petiolules on



A map of South America. The hatched portion represents the distribution area of *S. andigenum* corresponding to the 8000 ft. contour of the Andean range. The blackened portion represents the distribution area, according to Bukasov, of *S. tuberosum* in Chile and Chiloé. The letters A to N refer to the regions in which the collections were made (see text, p. 14). The dotted lines represent State boundaries.

The numbers are those by which the different varieties are distinguished in the collection. The numerals in brackets, e.g. 507(1), indicate that the specimen is a seedling of 507.

State and Region	Province or District	Map Ref.	Group I	Group II	Group III	Group IV	Group V	Group VI
Colombia:								
Central	Boyaca Cundimarca Caldas	A	—	1055, 890, 894, 977, 978, 1052	B7391, 888, 1063A	913, 997, 893, 889, 926, 998, 893A, B7387, 892, 903, 965, 924, 889(1)	914, 915, 1054, B7455, 904B, 903A	1061, 1031
South	Cauca Narino	B	—	—	895	1002A, 896, 897	—	—
Ecuador:								
North	Imbabura Pichincha Napo-Pastaza	C	—	—	—	—	—	—
Central	León Tungurahua Chimborazo	D	—	—	B7154, 709, 770	—	—	—
South	Cañar Azuay	E	634, 635	626	B7118, 624A, 633	B7112, 628, 641, 643, 643(1), 624C, 643(2), 624, 625, 640, 769, 632, 627	623, 638, 639	633A
Peru:								
North Central	Libertad	F	—	—	—	—	—	—
Central	Lima Junín	G	—	—	576B, 568A(2)	568A(1), 507(1)	507(2), 507(3)	1091
South Central	Cuzco Apurímac Ayacucho	H	—	—	—	429(1), 429(2)	—	—
South	Arequipa Puno	I	55, 56, 58, 68, 708, 699	67, 65, 576B, 764	—	207	—	—
Bolivia:								
North	La Paz	J	60, 61, 200, 212, 191	388, 215, 220, 218	—	194, 204	—	—
North Central	Cochabamba Oruro	K	241, 256, 281	226, 228, 251, 279	156, 236	154, 155, 282	—	—
Central	Chuquisaca Potosí	L	B6131, 133, 134, 136	—	132, 138, 139, 127, 130	129, 170A, 170A(1), 170A(2), 170A(3)	—	—
South	Tarija	M	146, 143	140, 141, 142, 149	145, 147, 148, 150, 151, 152, 153	—	—	—
Argentina:								
North	Jujuy	N	89, 91, 111, 106	110	90, 101, 102	100–	—	—

which the leaflets are mounted, are distinct and of medium length: that is, they are both relatively and absolutely shorter than those in Group III, and longer relatively than those generally found in Groups V and VI.

Secondary leaflets are in most cases but few and small, and are generally directly attached to the rachis. The leaf is a fully 'open' one.

The haulms of the varieties which fall into this group, like those of Groups II, III IV and V conform in varying degree to the *S. andigenum* type; that is to say, they possess multiple thin stems, with long internodes; they are usually about 2 to 3 ft. long and tend to sprawl.

The simplest, and possibly the more primitive type, is seen in Fig. 4. The leaves outlined in Figs. 5 and 6, with their greater number of secondary leaflets, present an increasing development in the size and complexity of the leaf, and a transition to the next Grade.

Group II. In this group the leaves as a whole are bigger, and the individual leaflets are definitely larger than those to be found in the preceding group. Five pairs of primary leaflets is the rule, which tends to give the leaf as a whole a somewhat elongated shape, though not in so pronounced a degree as that commonly seen in Group III. The primary leaflets, as in Group I, though sharply pointed, are relatively broader. The petiolules are similar to those in Group I.

Secondary leaflets are more numerous and larger than in the preceding group. The leaf is 'open' (cf. Figs. 7, 8).

The characteristics of this group present a straightforward development of those described in the preceding one.

Group III. The varieties included in this group all possess a large and markedly elongated leaf. This is due to the greater length of the internodes, a feature which brings about a separation, often pronounced, of the primary leaflets, each one from its successor. Hence there is not only no overlapping of leaflets, but there is often a wide gap between the adjacent border of two successive laterals. This disarticulation of the leaf is further emphasized by the extraordinary length of the petiolules to be found in this group. The leaflets themselves are broader than in those of preceding groups, and not so acutely pointed; they are set on the rachis at an angle of about 70°. Inasmuch as six pairs of leaflets is the rule, the whole leaf becomes drawn out; examples have been met which are nearly a foot long and but 4½ in. broad (cf. Figs. 9, 10).

Secondary leaflets are numerous and, owing to the long petiolules, they may be distributed either on the rachis or as acroscopic and basiscopic appendages to the petiolule. In this way a picture of great complexity, as in Fig. 10, may be developed.

Notwithstanding the excessive development of secondaries, the leaf remains 'open' or intermediate. The rachis is stouter in this than in the preceding group. Although the standard type of Group III, as shown in Figs. 9 and 10, is distinctive, this group, like the preceding, is not uniform, and varieties have been included which link it both with the groups preceding and following it.

In this group the haulms and habit are of the accepted *S. andigenum* type, but there may be divergencies here too: thus in the variety whose leaf is depicted in Fig. 10, the characters of the haulm and its habit are reminiscent of that of the *S. tuberosum* varieties. The group is distributed throughout the whole area but is not so common as the one following.

Group IV. This is the largest and most widely distributed of all the six groups, and at the same time the most variable. Its members are distinguished from those in Group III by the relatively short length of the petiolule, the lesser length of the internodes of the rachis, and the greater width of the primary leaflets.

There are usually four pairs of primaries: in most cases the leaflets are set at an acute angle with the rachis, and some slight overlapping is common, but the leaf as a whole still remains 'open'.

Secondary leaflet development is extremely variable; they usually spring directly from the rachis: in some varieties they are scarcely developed; in others they may be fairly numerous and of good size.

The leaf as a whole is both relatively wider and generally shorter than those of Group III, and hence it approaches the type which is commonly met with in the European domestic varieties (cf. Figs. 11–13).

This group contains those varieties which, by reason of their leaf characters, are in a somewhat intermediate position between those varieties contained in Groups I–III, all of which are unquestionably assignable to Bukasov's *S. andigenum* species, and those in Groups V and VI whose leaf characters are indistinguishable from those commonly found in the European family of potatoes.

Group V. Here are collected those varieties from the *S. andigenum* area whose leaves are such as might be, and are, found in very many of our domestic forms. In general, the leaves are large in area, broad in relation to their length, the whole assuming a polygonal shape. The leaflets are relatively broader than in any of the varieties of the previous groups and are usually acuminate, but the apical process is short; the base on either side of the petiolule is rounded and forms a sort of free lobule: that on one side, usually the more distal, is shorter than the other. Similar but less well-developed basal lobules may be met with in the other groups, but their occurrence is rare and they are not asymmetrical as in Groups V and VI.

Secondary leaflets have been present in all cases so far encountered, but their development has not been such as to occlude all the space between the rachis and the leaflets and thus convert the leaf to the 'closed' form (cf. Figs. 14–16).

Only one considerable difference between the leaves of this group and the next has been observed, and that may not be sufficiently constant to be of much value: it is that amongst varieties in Group V the primary leaflets either do not overlap, or only sufficiently so as to engage a narrow peripheral margin of each, whilst in Group VI the overlap is generally considerable.

Group VI. The leaves of any of the varieties forming this, our last group, could be matched line for line with one or other of our best known European varieties. They have these features in common: the leaf is big, wide, and polygonal in shape; the primary leaflets are large and broad, broader relatively than any to be found amongst the varieties in Groups I–IV. A characteristic feature is that the successive lateral leaflets overlap each other; this, as we have seen, may also occur in Group V, but it is more developed and more general in members of this group. In respect to the shape of the leaflets, their apices, and the presence of asymmetrical lobules at the base of the leaflets, there is no difference between the leaves of varieties in this, as compared with those in Group V. As only four examples have so far been encountered, it is not possible to say whether the leaf may show as many variations of detail as are to be found amongst our European varieties. The two tracings (Figs. 17, 18), however, display a remarkably wide divergence of pattern.

Secondary leaflets are very variable. Some varieties may be almost devoid of them (Fig. 18); others are well furnished. The leaf may be either open, intermediate, or closed.

The distinction between Groups V and VI does not rest with the leaf types, though minor differences can be observed. The real distinction between the two groups lies in the fact that the members of Group VI, in their habit and the character of their haulms, do not differ materially from those of the generality of our domestic potatoes, whilst those of Group V are nearer akin to the *S. andigenum* type by reason of their more numerous stems, bushy growth, and often sprawling habit.

It should be stated that of the four varieties which have been included in Group VI, throughout the whole area of distribution, three only have been grown in the open in England, and their habit of growth observed by the writer.

The six groups within which all the varieties of the Cambridge collection from the great Andean potato fields find their place, can be regarded as a regular series of successive types which, beginning with outspoken *S. andigenum* characters, end in the type of potato we know so well in Europe, and which we are accustomed to regard as a distinct species bearing the name *S. tuberosum*.

Dr Hawkes has subdivided the areas from which the varieties were collected into regions which are shown on the map (p. 10), and which are designated by the letters A to N. As the number of varieties involved is small, it was thought best for the purpose of comparing the incidence of the various groups, to consolidate districts into the following areas:

1. Colombia	i.e. Regions A and B
2. Ecuador	Regions D and E
3. Central and South Peru	Regions G, H and I
4. North and Central Bolivia	Regions J, K and L
5. Southern Bolivia and Northern Argentine	Regions M and N

In Fig. 2 the disposition of the varieties of each area between the various Groups I–VI is shown diagrammatically. It will be observed that in Area 5, only 5% of the collection falls into any group lower than III, and actually none into Groups V and VI; that the farther the area is from Southern Bolivia, the greater the number of varieties which find their place in the IV, V and VI Groups. In the most distant area, Colombia, there are no varieties belonging to Group I, whilst about a quarter of the collection falls into Groups V and VI.

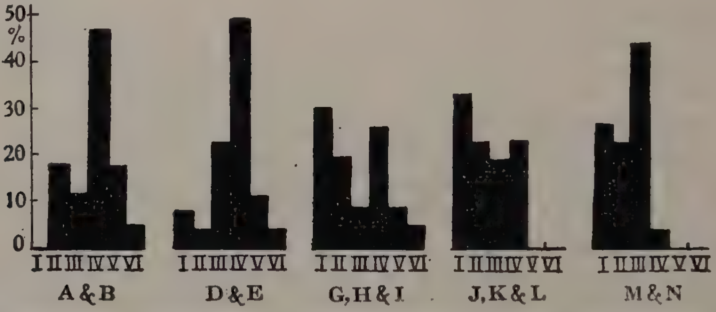


Fig. 2. Graph showing the incidence of the varieties of *S. andigenum* in Groups I–VI in the different regions, from whence the Empire Collection acquired them.

It has already been explained that Group IV contains those varieties whose leaves are transitional between the commonly acknowledged types of *S. andigenum* represented in Groups I–III, and those of *S. tuberosum* placed in Groups V and VI respectively.

If the varieties which fall into Groups IV–VI be compared with those which fall into Groups I–III in each of the five areas, we obtain a picture in which the incidence of the strictly *S. andigenum* types and those either approaching to, or identical with, that common to *S. tuberosum*, are sharply contrasted. In Fig. 3 we have such a set of graphs, and it will be seen that the increased incidence of *S. tuberosum*-like forms (black) steadily increases from 5% in Southern Bolivia, and Northern Argentina, to 27% in Central and Southern Peru, to 65% in Ecuador, and to 70% in Colombia.

It has been stated by Bukasov, and it is generally accepted, that the centre of distribution of the *S. andigenum* species is in the region of Lake Titicaca; it will be seen that the incidence of the groups is such that the I–III Groups occur most freely in this district, and that the further we recede from that centre, the greater is the incidence of the IV–V Groups, till some 1500 miles to the north, a few varieties of unquestionable native origin are cultivated, which have all the essential characters of *S. tuberosum*.

Before we venture on an explanation as to how and why such a change in the distribution of the group took place, we must remember that according to the Russian observers, all the cultivated varieties grown just 1500 miles to the south of Lake Titicaca, i.e. in Chiloé and Chile, belong in the strict sense to the species *S. tuberosum*.

Whether this latter statement is to be taken as literally true could only be established by an examination of a representative collection of varieties from the Chile-Chiloéan area; such has not, as yet, been available to the writer. Amongst the few varieties from Chile which have been grown at Cambridge, one named 'Pichuna' has a leaf which accords well with the standards set out for Group IV, whilst its habit of growth is much nearer that of a *S. andigenum* than a *S. tuberosum* type. Two others, on the other hand, resembled our domestic potato plants, both as regards leaf and habit.

That the overwhelming majority of the potatoes in the Chiloéan area are of the Group VI type, even if they originated from the same centre of distribution as the *S. andigenum* varieties where Group VI is rare, would be no matter for surprise, if we assume that there is some selection value in the leaf type of Group VI in a 'long day' humid environment.

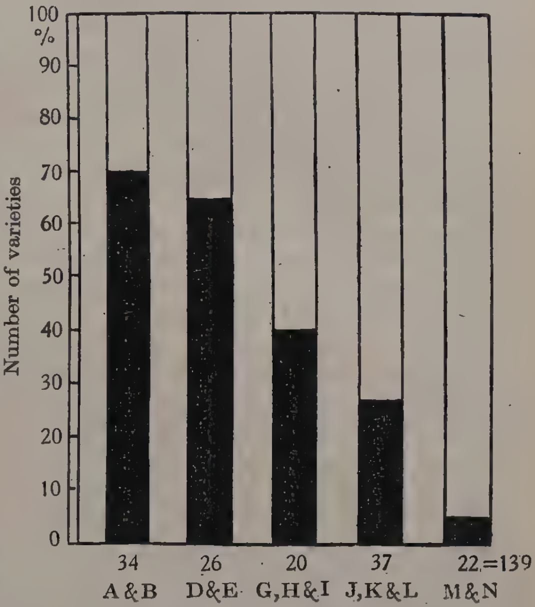


Fig. 3. A graph showing the incidence of the varieties of *S. andigenum* of Groups I–III, white, and Groups IV–VI inclusive, black, included in Fig. 2.

How the potato reached the Chilean area is still an open question. Wight's (1917) view that it was brought there by man in the relatively recent Inca time is, as Hawkes (1944) has shown, unlikely, seeing that the Araucanian name for a potato, 'Pogni', differs completely from either the Quichuan 'papa' used by the Incas, or the old Aymara term 'choque'. Hawkes thinks, and the writer agrees with him, that the 48 chromosome potato of the Chiloéan region was introduced by man long before, possibly several thousands of years before, the Inca period, and that it there underwent a process of selection in regard to its photoperiodic reaction and cropping capacity, resulting in a high degree of uniformity of its physiological and associated morphological characters. This process was rendered possible by the strict geographical isolation of the district which, cut off by the Atacama desert in the west, and the Andes on the north, could only be approached by high and difficult mountain passes on the east.

Hawkes further points out that, whilst it is almost certain that the original $2n=48$ *S. andigenum* species arose from the doubling of one or more of the $2n=24$ species in the Lake Titicaca region, such as *S. stenotonum*, in Chile and Chiloé there are no representatives of the $2n=24$ group of species at all; hence its $2n=48$ varieties must have been derived from the pool of potato material in the north.

The further question arises as to what were the forces which were responsible for the specific patterns of distribution of the cultivated *S. andigenum* varieties described above, a distribution in which the more *S. tuberosum*-like leaf types represented in Groups IV–VI tend to separate out at either fringe of the distribution area. It is suggested by the writer that the bigger, more developed leaf character of these groups has a selection value in both the north and south of the area, because it is better adapted to the heavier rainfall and moister atmosphere encountered in these regions. Hawkes looks to man as the main and perhaps the sole agent responsible for the pattern of distribution and, in support, adduces ample evidence to show that in the past, and to a much greater extent in recent times, cultivators have made a practice of growing these large-leafed types in Colombia and Ecuador because they are better yielders and possess in greater degree than the others, the qualities they desire.

Whether the peculiar distribution of the types is independent of man, or results from a happy coincidence of man's desires and Nature's dictates, the result is the same: a sorting out of a specialized *S. tuberosum*-like type of potato at either end of the South American continent. In other words, the *S. tuberosum* varieties are merely derivatives from the original stock of $2n=48$ potatoes growing in the Andes which has been described by the Russian observers and called by them *S. andigenum*. There are not two species of domesticated $2n=48$ potatoes, but one, and that one is *S. andigenum*.

That such a conclusion creates a new and serious difficulty for the systematist cannot be overlooked. The European potato has enjoyed the name of *S. tuberosum* for over 300 years; the potato of Chile, by reason of its morphological affinities has, of recent years, assumed the same. The Russian workers have described a huge family of Andean potatoes to which they were entirely justified in giving a new name, *S. andigenum*. One can only apologize to the taxonomist and trust that he will find a solution to this rude upheaval of acknowledged precedence, so soon as he has satisfied himself of the cogency of the evidence, which would prove that from the strictly biological point of view *S. andigenum* is not only the accepted term for a widely distributed and geographically differentiated species, but that the European potato is directly derived from it, and has no inherent claim, based on biological merits, to a distinctive specific title.

We may now turn to consider what were the characters of the original potato introduced into Europe, and from whence did it derive.

In Table 1 there are set out the characters, so far as they can be ascertained from the accounts which have come down to us, of the potato varieties known and described by botanists and others between the years 1588, the date on which Clusius received his first tubers from the Papal Legate, and 1651, when J. Bauhin's *Historia* was published. It will be seen that four different varieties can be recognized: all four were vigorous growers, the stems often attaining 5 or 6 ft. in length; all tend to sprawl and form a bushy growth. The flower colours are white, heliotrope or purple, all of which are common to the *S. andigenum* varieties.

Of the leaf we learn that the number of primaries was variable, as was the development of secondaries; the latter, however, seem to have been neither numerous nor large enough to attract much attention.

When one turns to the contemporary illustrations of the haulms that have come down to us, it is obvious that the woodcuts of Clusius, Gerard, Bauhin and Parkinson are all schematic and conventionalized, and are of little value from a taxonomic point of view. There is, however, one most important exception. As is well known, Clusius received his potato tubers from Philippe de Sivry, the Lord of Walhain and Governor of Mons in Hainault, Belgium, who, in turn, had obtained them from a friend of the Papal Legate in Belgium; these tubers were received whilst he was in Vienna, but were grown at Frankfurt-on-Main. Clusius caused an aquarelle to be made of his precious plant; this coloured drawing was preserved at the Plantin Museum. An exact copy of this drawing is reproduced by Roze.[1] Here we are dealing with both a work of art and a naturalistic representation, in which detail has been carefully studied.

The plant has a stout stem, bearing a long pedicel surmounted by a group of heliotrope flowers, very similar in shape and colour to that found in the variety 'Up-to-Date';

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[1] Thanks to Mr Savage, Librarian of the Society, I have been able to confirm this statement, by comparing it with a photograph of the original aquarelle in his possession.

attached to the inflorescence is a spherical berry. Three leaves are represented, and although the distal end of the apical leaflet of each is cut off by the margin of the drawing, the character of the leaf, as a whole, as well as its details, are readily appreciated. A tracing of one of the leaves is reproduced in Fig. 1 (on p. 4).

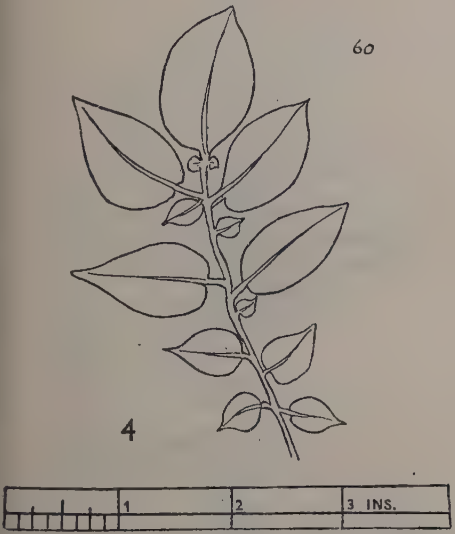

Fig. 4. The variety 'Chiar Imilla', black girl, from La Paz, Bolivia. An example of the Group I type of leaf.

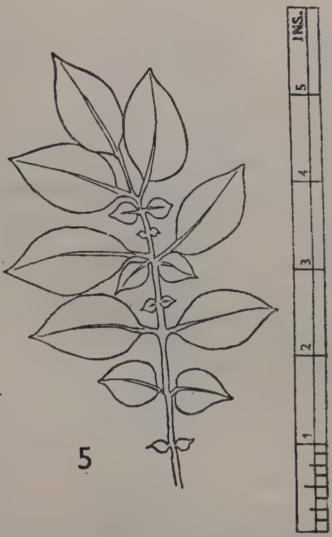

Fig. 5. The variety 'Papa Runa Cala' from Tarija, Bolivia. An example of the Group I type of leaf.

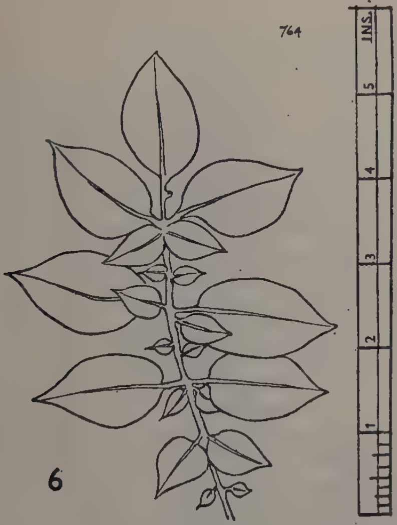

Fig. 6. A variety from Pancartambo, near Cuzco, Peru. An example of the Group I type of leaf.

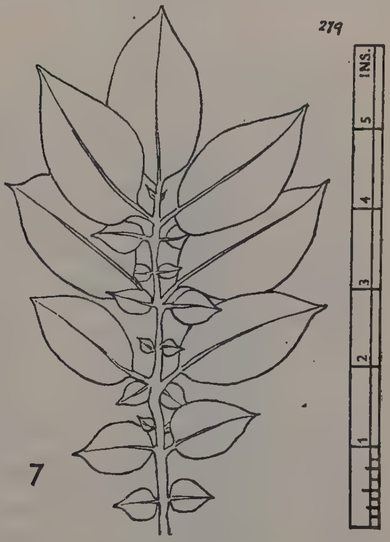

Fig. 7. A variety 'Puca Imilla', red girl, from Cochabamba, Bolivia. An example of the Group II type of leaf.

It will be observed that this leaf is composed of four pairs of primary leaflets, between which are two pairs of small, broad, rounded, sessile secondary leaflets. The primary leaflets are rather narrow, and their apical processes scarcely developed. More important is the fact that the primary leaflets are inserted widely apart on the rachis, and that there is no suggestion of overlapping. The whole leaf is long and narrow, and widely 'open'. According to the classificatory scheme here adopted, such a leaf would undoubtedly be placed in Group IV and, as such, differs considerably from the *S. tuberosum*

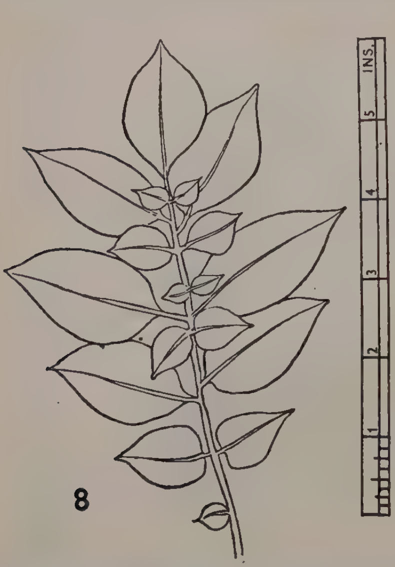

Fig. 8. A variety 'Papa Runa Morada' from Tilcara, Jujuy, Argentina. An example of the Group II type of leaf.

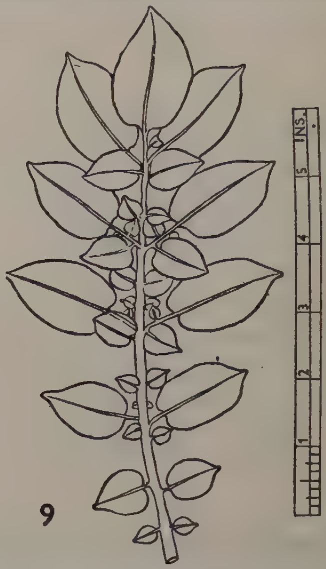

Fig. 9. A variety 'Sabancra' from Central Colombia. An example of the Group III type of leaf.

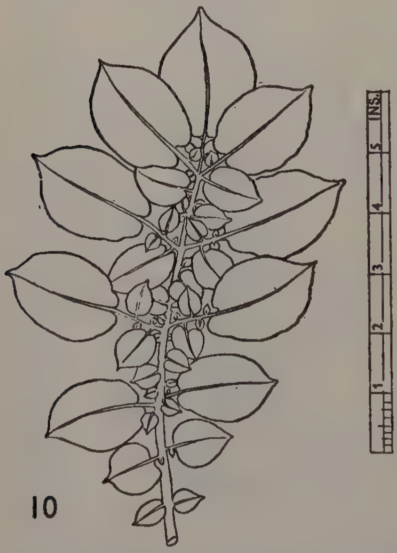

Fig. 10. A variety 'Jubalena' from Yurakpungo, Canar, Ecuador. An example of the Group III type of leaf.

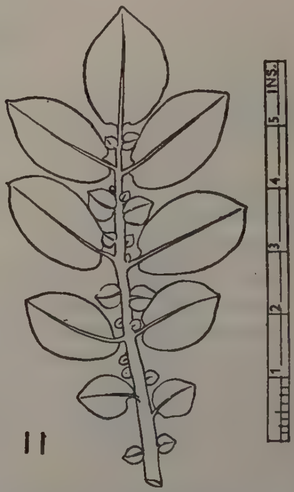

Fig. 11. A variety 'Arbolona', from Sote, Boyaca, Colombia. An example of the Group IV type of leaf.

type of leaf to which we are accustomed. Indeed the leaf bears a strong resemblance to varieties grown in Colombia, such as 'Arbolona' in the Boyaca province (Fig. 11), and 'Lizaraza' in that of Cundimarca, both of which are included in this group.

That the stem and rachis of Clusius's specimen are represented as short and fleshy does not exclude it from the *S. andigenum* species, even if in the majority of *S. andigenum* varieties they are thin and rather woody. It is recorded in the field book of Dr Hawkes that in eight of the *S. andigenum* varieties encountered in this expedition, the growing specimens had remarkably thick stems. Three examples occurred in Group III, four in Group IV, and one in Group VI. Five of the eight come from the northern and one from the southern end of the distribution area; the remaining two were found in South Central and Southern Bolivia respectively. It would appear that this 'tuberosum-like' feature also tends to be commoner at the periphery of the species' habitat.

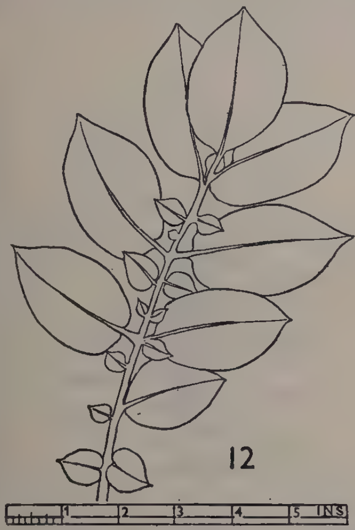

Fig. 12. A variety 'Argentina' from Zipaquira, Cundinamarca, Colombia. An example of the Group IV type of leaf.

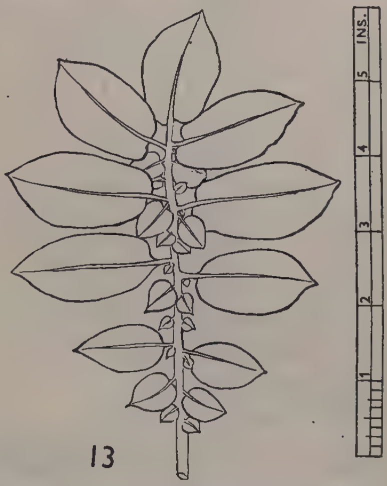

Fig. 13. A variety 'Pali', from Sucre, Bolivia. An example of the Group IV type of leaf.

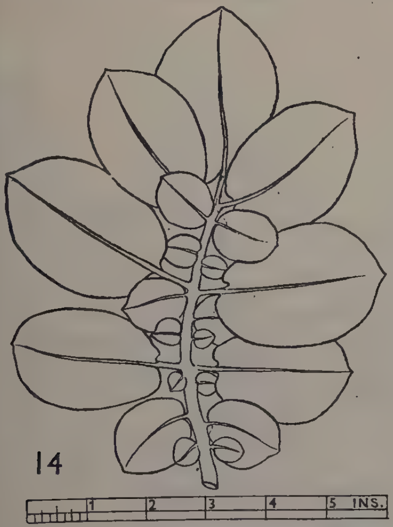

Fig. 14. A variety, a seedling of 'Argentina' from Caldera, Cundinamarca, Colombia. An example of the Group V type of leaf.

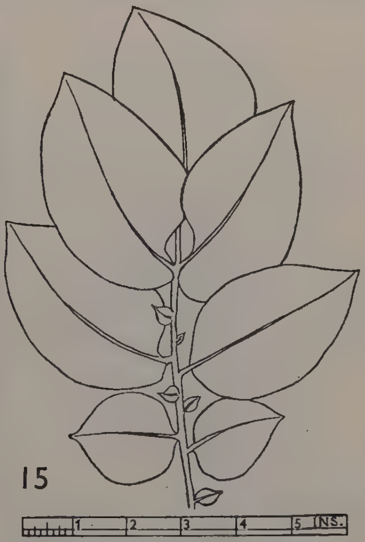

Fig. 15. A variety 'Quesillo' from Yurakpungo, Canar, Ecuador. An example of the Group V type of leaf.

When attention is turned to the underground parts of these early potatoes, we find several interesting features which differentiate them, in degree rather than in kind, from present-day European varieties. They are all late, indeed extremely late varieties; two seedlings amongst them never came to tuberization at all. In the early accounts it is frequently stated that it is desirable to leave the potatoes in the ground till the tops are cut down by frost, which implies that tuberization was generally slow and did not take place until the days grew shorter. In fact, these early varieties were what we now speak of as short-day varieties and behaved as do most *S. andigenum* potatoes when grown

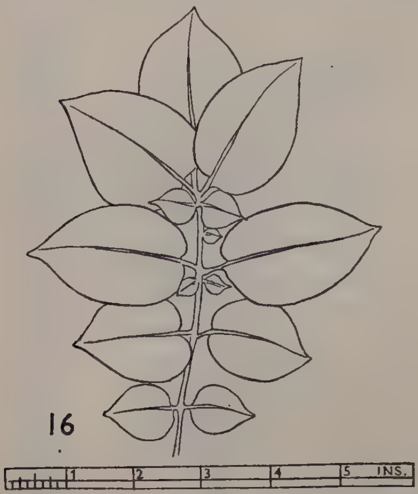

Fig. 16. A variety 'Imilla blanca', white girl, from Cochabamba, Bolivia. An example of the Group V type of leaf.

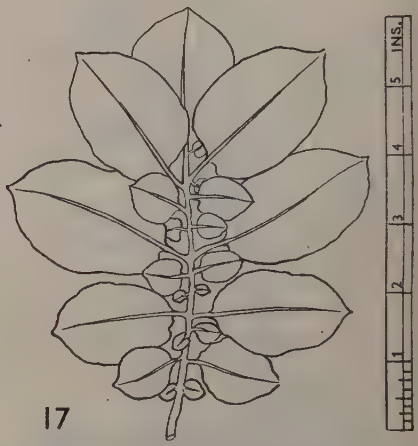

Fig. 17. A variety 'Lanta Mari' from Puno Peru. An example of the Group VI type of leaf.

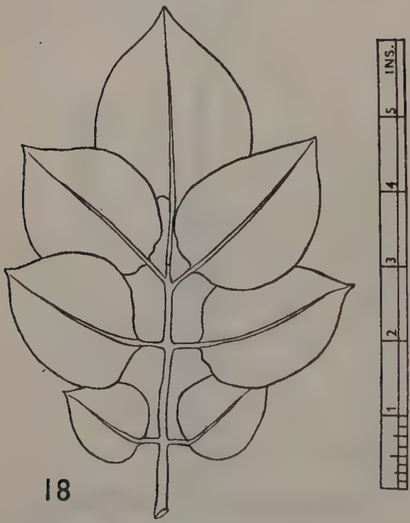

Fig. 18. A variety 'Chaucha Blanca', from Huangarcucho, Azuay, Ecuador. An example of the Group VI type of leaf.

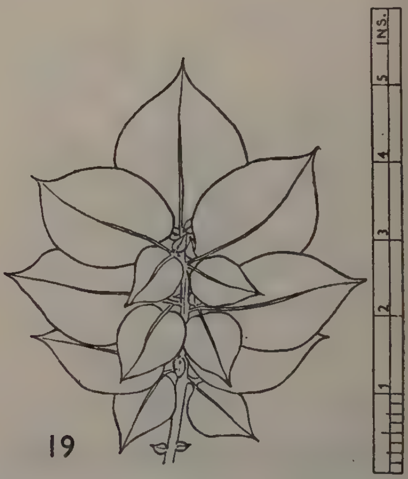

Fig. 19. The English variety 'Lochar', illustrating the 'closed' type of leaf.

in our country. It was not till considerably later that early and maincrop varieties came to be developed in Western Europe.

One of the most important observations made by the Russian scientists as a result of their South American expeditions, was that the potatoes of the Andean region were, as a whole, 'short-day', and those of the Chilean region 'long-day' varieties. Inasmuch as the European potatoes are to-day all 'long-day' varieties, they assumed that the latter could only have been derived from a region where such types flourished. This argument would appear to be fallacious for the following reasons. Whilst the great majority, viz. 34, of the Peru-Bolivian collection of *S. andigenum* varieties examined are, as Driver & Hawkes (1943) have shown, 'short-day' types, one 'long-day' variety and nine

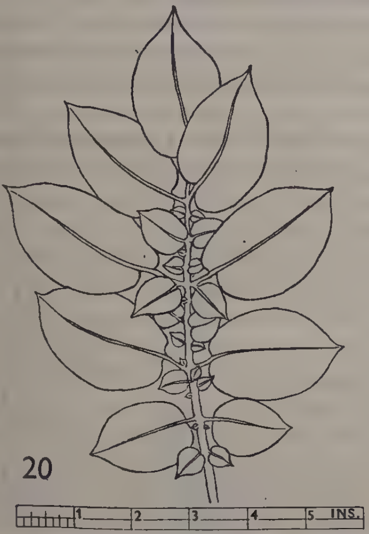

Fig. 20. The English variety 'Majestic', illustrating the 'intermediate' type of leaf.

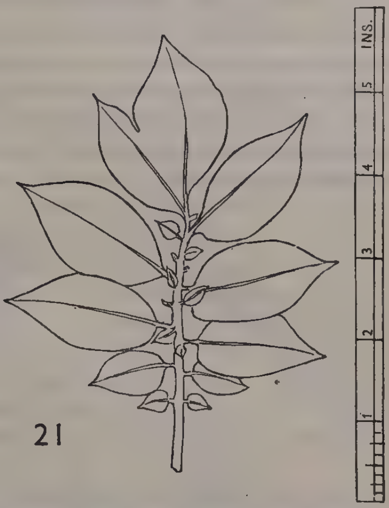

Fig. 21. The English variety 'King Edward', illustrating the partially 'open' type of leaf.

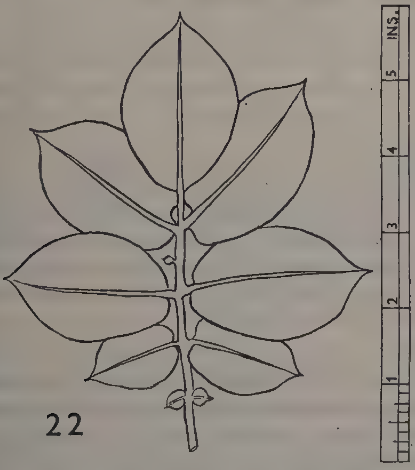

Fig. 22. The Dutch variety 'President' (President Kruger), representing the completely 'open' type of leaf.

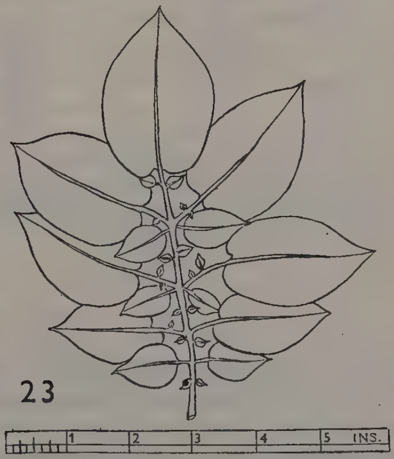

Fig. 23. A seedling from the mating 'Abundance' × 'Flourball', with well-developed secondary and tertiary leaflets and exhibiting the 'intermediate' type of leaf.

whose reactions lay between the two, and hence are termed by them ‘neutral’, were found.

It has been shown by the writer that cropping is controlled by genetic factors (Salaman, 1924), and later it was suggested that these may, in reality, be genetic factors concerned with the physiological reaction of the plant to the available daylight afforded by its environment. If that is so, and short-day reaction is, as Hackbarth (1935) has shown, a dominant, then the segregation of reactive types will occur as a result of breeding and thus afford the opportunity for the creation of long-day types from what are phenotypically short-day forms.

Not only were the early introductions very tardy in their tuber formation, but their tubers when formed were small and extremely numerous, fifty or more to a root being a common experience.

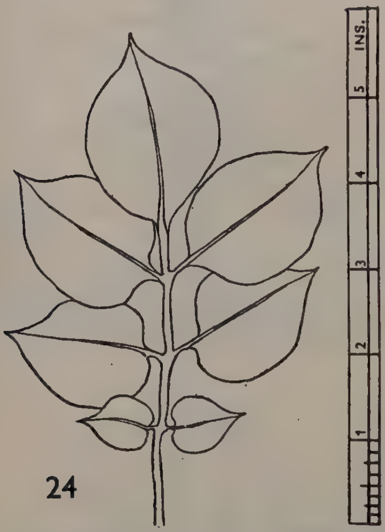

Fig. 24. A seedling sister to the above, raised at the same time and in the same place, devoid of all secondary leaflets, and exhibiting the completely ‘open’ leaf.

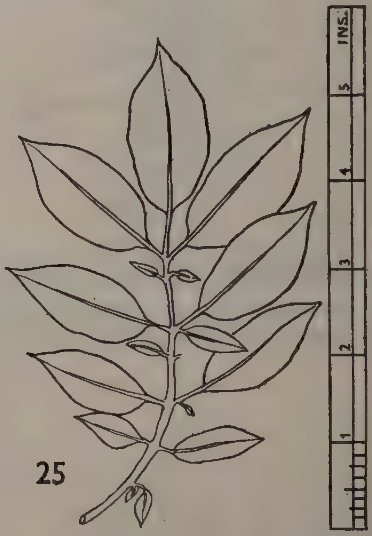

Fig. 25. A seedling from the mating ‘Paterson’s Seedling’ × ‘Pepo’, exhibiting the elongated completely ‘open’ leaf, the long, narrow, pointed primary leaflets and poor development of secondary ones, characteristic of the Group I of the *S. andigenum* collection of varieties.

When the writer was engaged on the genetics of the interspecific crosses (Salaman, 1929) between the domestic potato varieties and *S. demissum*, it was frequently found that seedlings occurred which developed enormous tops, often 6 and 7 ft. long, and correspondingly bulky, but even when such were left in the ground till December their crops of tubers were not only extremely late in forming, but their actual bulk was relatively insignificant, whilst the number of small tubers of which they were composed was often greater than fifty.

Another feature of the early sixteenth-century European varieties was the length of their stolons: this is often mentioned in the writings of the period, and is invariably shown in the illustrations. Driver & Hawkes (1943) point out that the *S. andigenum* ‘short-day’ varieties, when grown in a ‘long-day’ environment, develop long stolons. In Europe breeders have steadily eliminated long-stolon plants, and by so doing have brought their new seedlings into harmony with the correct tuber-bearing reaction necessary for good cropping in their new environment.

All these characters which distinguish the earliest introductions from the potato of to-day were, in fact, the reactions of a 'short-day' plant, doing its best to survive in a 'long-day' environment.

A constant feature of the early introductions was the irregular 'knobbly' appearance of the tubers, and the great depth of their eyes. Both these characters are extremely common to-day amongst the typical *S. andigenum* varieties. The large, smooth, handsome tuber we expect to-day, is a relatively recent acquisition which has been obtained by breeders consciously working to that end.

The interest aroused by the discovery of so many new potato species by the Russian, Swedish, German and English expeditions, has led to extensive research directed towards the incorporation into our domestic stocks of some of the more desirable characters one or other of these may possess, such as absence of dormancy, with the possibility of raising two crops in the season; the possession of high starch or nitrogen content; resistance to frost and to attacks of *Phytophthora infestans* and virus infection. It has been found that none of the *S. andigenum* stocks is in a position to offer us any quality not already available in one or other of the European potato stocks. The *S. andigenum* varieties are as susceptible to frost, virus disease and blight, as are any of the old European stocks and, like them, they include both wart resistant and wart susceptible varieties. This absence of any new or valuable quality has come as a disappointment to those who regarded *S. andigenum* as a species distinct from *S. tuberosum* and our domestic stocks. But should it not rather be regarded as evidence of its common ancestry with our European stocks?

Once the potato was established in Europe, its propagation by tuber was the recognized method of reproduction, but that did not exclude the raising of seedlings by persons specially interested. So soon as this occurred, it is obvious that those seedlings which failed to form tubers, would be discarded, and those which did, and whose tubers were of a goodly size and shape, would be selected and grown. In this way maincrop varieties arose which gradually replaced the very late croppers of the first fifty years. Before very long it must have been obvious that early varieties could also be secured by selection of suitable seedlings. Such early selections were undoubtedly based on families raised from selfed seed, and hence the wider variations which cross-fertilization renders possible, did not make their appearance until the potato had won its place in the dietary of the people, and demands for particular types, for specific purposes, came to be enunciated. It might be thought that it would take many generations of breeding, when neither hastened by hybridization nor by purposive selection, to convert a Grade IV *S. andigenum* plant, with its appropriate foliage and habit, into one of Grade V. Such is not the case. In a preliminary experiment made some ten years ago, a selection was made of the most *S. tuberosum*-like individual seedling in a selfed seedling family of a Peruvian variety. This was selfed again and in the following year the most *S. tuberosum*-like seedling once more selected; the progress attained in that short time, so far as foliage characters were concerned, was remarkable. Unfortunately the work was interrupted and has not been resumed.

Evidence of similar segregation is to be found in the material under examination. In two seedling varieties the parent forms were of Group IV, and their five seedlings conformed to the same type. In another of these, where the parent form was not included, the seedlings fell into Groups III and IV, and in a second, into Groups IV and V.

The extent to which the leaf characters are genetically controlled has been already referred to, but one has no need to employ wide interspecific crosses to demonstrate this fact. Variation of a large order can be observed without going outside the range of our domestic European varieties. In Figs. 23 and 24 are shown tracings of the leaves of two seedlings of the cross 'Abundance' × 'Flourball', from which it will be observed that one is devoid of secondary leaflets, whilst in the sister seedling of the same family there are secondaries and tertiaries on the rachis, and acro- and basiscopic leaflets on the petiolules. A more remarkable example of the segregation of leaf character is shown in a family derived from 'Paterson's Seedling' crossed by 'Pepo'. As far as can be ascertained, there is no recent American blood in any of the forbears[1]; yet the whole family displays, in varying degree, pronounced *S. andigenum* characteristics in its foliage, the commonest of which is the reappearance of the small and elongated Grade I type of leaf, with its sharply pointed and narrow leaflets, a complete absence of overlapping, and a poor development of secondary leaflets, all mounted on a tenuous rachis (Fig. 25).

We are now in a position to state that not only is there no intrinsic difficulty in deriving our European potato from *S. andigenum*, but that there exist to-day, and presumably did so 350 years ago, varieties of potato in the northern parts of the distribution area of *S. andigenum* which are, in the character of their leaf and the habit of their growth, similar to those now growing in Europe, and that in respect to their reaction to length of day as it affects stolon and tuber formation, the majority of them probably behaved as did the earliest introductions of which we have records.

So far, then, as the biological arguments go, Colombia afforded to the introducer of the potato, not only an accessible but a suitable source of varieties, from which the European potato could be developed by selective breeding.

We must now consider the historical and political data which are relevant to the problem under discussion. The first step is to ascertain as nearly as possible the date of the first introduction of the potato to Europe. We are on safe ground in assuming that this took place in Spain, the only country which enjoyed any contact with the western parts of South America between the critical years of 1550 and 1570.

In 1564 Clusius visited Spain for the purpose of describing the rare plants to be found there, and published his results in 1576. In that work there is no mention of the potato. From this we may conclude that it was not there in 1564, and that between then and 1576, its cultivation, if any, must have been but local and insignificant or it would scarcely have escaped the attention of so careful and industrious a savant.

The writer has, in an earlier communication (Salaman, 1937), told how the potato was being eaten in the wards of the Sangre Hospital at Seville in 1573 and assuming, as there is good reason to do, that the stocks were raised locally, it may be taken that the potato must have reached Seville at the very latest in 1570 and hence have left South America not later than 1569.

If the Russians are correct in their view that the potato of Europe must have been introduced from the Chilean area, and that a Peru-Bolivian source is unthinkable, then it is necessary to inquire into the possibility of such an introduction being effected in 1569, or a year or two earlier.

No journey was made from Chile direct to Europe via the Magellan Straits till 1579, so that the potato could not have come that way, even had Sarmiento not been completely cleared out of stores before he left the Straits. It could not have been taken from South Chile till that part of the country was reached by Mendoza in 1559, when Chiloé was first sighted. This island was not occupied, however, till 1565. From 1559 till 1565 there was ceaseless warfare between Spaniard and Araucanian on the mainland north of Chiloé, and no real progress was made southward although the Spaniards founded the town of Valdivia over 100 miles to the north of Chiloé in 1553. From 1565 onwards their hold on the country was tenuous in the extreme, fighting for every inch of land, losing it one day to recover it the next; the war continued till 1568, when, after a disastrous defeat, the Spaniards called a truce which lasted till 1572. In 1570 occurred the great earthquake which destroyed Concepcion and most of the southern settlements. From 1572 the fighting was spasmodic, but taken up in earnest again in 1576. After 1576, internecine warfare broke out again, and lasted, off and on, for the next 200 years; but Spain already had the potato growing, and the patients of the Sangre were enjoying them in 1573.

[1] 'Purple Chile' was the great-great-great-great grandfather of 'Pepo'.

The potato apparently did not appeal to the Spanish conquerors in Chile as a food substitute during Valdivia's leadership, 1541–54. In a letter to Charles V dated 1551, Valdivia mentions the potato as one of the crops grown by the natives, yet when his own forces were in the direst want of food, and the daily ration measured by a few score grains for each man, neither then, nor later, when he grew crops of maize and wheat for his army's needs, does he make mention of the potato.

It is not claimed that it was impossible for a man to have put a potato in his pocket in Chiloé and to have brought it back to the more settled country in the north during this period, but it was, to say the least, no very happy time for the curioso to roam an enemy country for botanical specimens, especially as he had all the potatoes he needed in the settled hill country around Lima. But assuming that someone did deliberately export potato tubers from the Chiloé region at some date during the critical period we are discussing, how would the journey to Spain have been made?

The tuber would have been harvested in Chiloé in April and forwarded by boat to Lima—when such happened to be available. The sea voyage would take about 2 weeks. At Lima it would be a thousand chances to one that it got no farther, for, from the time of Valdivia's invasion in 1541 till well into the eighteenth century, Chile was regarded as a mere appanage of Peru and had no direct relation, official or commercial, with the outer world; its exports were consigned to the merchants of Lima, where, presumably, they were merged with the produce of Peru. Assuming, however, that some tubers did get forwarded after change of ship and only a couple of weeks' delay, they would have reached Panama 2 weeks later and then would have been carried by porters and mules a 3 days' journey across the Isthmus to Nombre de Dios. The arrival in Nombre de Dios might possibly have taken place as early as the end of June if all the connexions had been promptly made. Were a ship ready to start at once, the tuber might be landed at Seville before the end of September; too late, however, to be planted in the same year.

Assuming that the precious tuber had been kept as cool as possible during its journey through the tropics, and its long sea voyage through the warm waters of the gulf, and had, on arrival in Spain, been placed in a cool cellar till planting time in April, it would still have been out of the ground for about 12 months, a very long time for a tuber, even under the most favourable conditions.

It is not to be denied, however, that such a tuber might still give rise to a plant capable of yielding some sort of a crop, or a crop might have been raised from the secondary tubers which would have formed on the stolons arising from the outgrowing sprouts; in either case the problem would have been solved. But the chances of the tuber ever surviving such a journey or, indeed, arriving at all in Spain under the prevailing conditions, are so slender as to be scarcely worth considering.

What then, are the alternatives to a Chilean origin, with its wellnigh insuperable transport difficulties?

Potatoes were an everyday article of commerce and consumption in Lima and the northern ports of South America such as Payta, Tumbez and Buenaventura and, owing to the variety of climatic conditions at any one latitude, they could be grown at practically any time of the year. The journey from Lima to Nombre de Dios could be made in about 17 days and so arranged that the tubers might be taken on board at once; in this way they could have arrived in Spain in time to be planted in the early summer.

Another, and more likely route, is that the potatoes reached Cartagena in Colombia on the north-west Atlantic coast from the Bogota district. Already by 1549 a regular route had been opened between this port and the interior, and the journey from Bogota was accomplished in about 12 days. Every ship which sailed from Nombre de Dios en route for Spain called at Cartagena and stayed there 10 days, to receive the royal revenues and await the Margarita patache. It is possible that potatoes might have been taken on board at Cartagena as ship's stores for the journey home, although this was normally done at the next port, Havana.

The difficulties both of transit and season would, of course, have been surmounted at one stroke by anyone who had the genius to send home the true seed from the potato-berry, instead of tubers. Such seed might have come from a stray fruit in Chile, Peru, Bolivia or Colombia, and we have no proof that it was not so transmitted. There is, however, very good reason to doubt it. Had the potato come over as true flower seed, it is almost certain that for some time at least this method of propagation would have passed as the normal one for growing crops, and of such there is no evidence.

Indeed, against such a theory is the fact that neither Clusius nor any of the great herbalists make mention of it. It is true that Clusius sent true seed to his friend Hogelandius, but it will be recalled that the result was not very happy, for the seedling produced no tubers. It should be recorded that in Colombia a particular variety is, by way of exception, raised from true seed. Though this procedure is extremely rare, it appears to have a long tradition behind it.

The evidence from contemporary history which demonstrates the well-nigh insuperable difficulties of transporting Chilean potato stocks to Europe, in the period under discussion, thus adds material strength to the views presented here, based on a study of the Andean varieties of to-day, viz. that the potato which reached Europe in the latter half of the sixteenth century might, and possibly did, come from the northern end of the Andean area of distribution of the species *S. andigenum*. We may go further, and say that the most likely port of departure would have been Cartagena, and its most probable source those stocks which belonged to the Groups IV, V, or VI as described in this paper, cultivated by the natives near Bogota.

Summary

1. From an examination of 139 varieties of the species *Solanum andigenum*, it has been possible to establish on the basis of leaf characters six different intergrading groups which show a transition from what is regarded as a typical *S. andigenum* type, to one no less typical of the domestic European varieties commonly known under the specific name of *S. tuberosum*.

2. It is suggested that there is, in fact, one, not two, species of cultivated potatoes with the chromosome formula of $2n=48$, and that one is *S. andigenum*.

3. The use of the term *S. tuberosum* is convenient as indicating the specialization which has overtaken varieties derived from one of the *S. andigenum* group forms in Europe, and another in Chiloé and Chile.

4. That the place of origin of the European potato is to be sought for in the northern extremity of the distribution area of *S. andigenum*, and that Colombia is its most likely location.

5. That the potato left some northern port in South America, possibly Cartagena, and that at least one importation reached Spain at the port of Seville not later than 1569.

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A revision of the genus Harpochytrium. By FRANK W. JANE, Department of Botany, University College, London

[With 28 Text-figures]

[Read 8 February 1945]

Within recent years the opportunity has occurred to make a detailed study of the species of *Harpochytrium*, with the exception of *H. apiculatum*, and this has led to a revision of the genus, in which two new species are proposed, three accepted species reduced to forms of other species, and the so-called green species excluded.

PREVIOUS INVESTIGATIONS

Lagerheim (1890) gave the name *Harpochytrium* to a small colourless Swedish plant growing on *Hyalotheca dissiliens*. His description was brief and his figures of the sporeling and older plants were accurate. He did not show the relation of the *Harpochytrium* to the mucilage of the host plant. In the present paper the term 'host' is used to designate the plant on which *Harpochytrium* is lodged, with no suggestion of parasitism. Gobi (1887) had previously briefly described the same plant, without giving it a name; in 1899 he published a fuller description of the plant, which he found on various desmids and other algae with well-developed mucilage, and named it *Fulminaria mucophila*, a curious fact, since he appears to have been fully conversant with Lagerheim's work.

Dangeard (1903) described a plant under the name of *Rhabdium acutum*, which appears to be identical with the one which Wille (1900) had already named *Harpochytrium Hedinii* from Tibetan material. Wille (1903) subsequently referred to this plant as *Fulminaria Hedinii*.

Atkinson (1903, 1904) published the first detailed account of the genus *Harpochytrium*: in it he included three species, *H. Hyalothecae* Lag. found in Europe and the U.S.A., *H. Hedinii* Wille, which was known to occur in Europe, Tibet, U.S.A. and Patagonia, and *H. intermedium* Atkinson, known only from the U.S.A.

Harpochytrium appears to have aroused little further interest until Scherffel (1926) described several species, including a plant which possessed a chromatophore, and which he named *H. viride*. Since then it seems generally to have been assumed that the algal affinities of the genus, suggested by Wille (1903), have been firmly established.

Korschikoff (1931) briefly described another colourless species from Russia, naming it *H. tenuissimum*.

The most complete account of the genus which has been published is that of Pascher (1938) in Rabenhorst's *Kryptogamen-Flora*. He divides the genus into two subgenera, *Chytridiochloris*, for the reception of the so-called *Harpochytrium viride* and *H. Scherffelii*, both pigmented plants, and *Harpochytrium* for the non-pigmented species, of which he recognizes five or six.

Finally, Jane (1942) described in some detail plants from North Wales which closely resembled *H. tenuissimum* Korsch.

AFFINITIES

Lagerheim (1890) referred *Harpochytrium* to the Chytridiales, a view with which Dangeard (1903) and Atkinson (1903) concurred. Fischer (1892), Schröter (1897) and von Minden (1915) all accepted the genus as chytridiaceous; Wille (1903), impressed by the resemblance to *Ophiocytium* and *Characium*, placed it among the algae, as a reduced type which had lost its chlorophyll; for its reception he erected a special family, the Harpochytriaceae; Wille's suggestion appeared to receive support from Scherffel's (1926) discovery of a tubular pigmented alga, which possessed a proliferating sporangium;

Scherffel named this plant *Harpochytrium viride* and it has since been accepted by many botanists as a member of the genus. The view now generally held (Printz, 1927; Fritsch, 1935; Gwynne-Vaughan & Barnes, 1937), is that the genus is algal, consisting in the main of reduced, unpigmented species. Gäumann & Dodge (1928) and Fitzpatrick (1930) regard the colourless species as fungi, while G. M. Smith (1933), by omitting the genus in his algal work, tacitly implies that he does not regard as algal the non-pigmented species which Atkinson recorded from the United States. Recently (Pascher, 1938; Jane, 1942) it has been questioned whether the genus, as at present constituted, is a natural one.

Gobi's (1899) extreme view, that *H. Hyalothecae* is not a plant, may be disregarded. While the reasons which led him to remove it from the Chytridiales merit consideration, it is difficult to avoid the conclusion that he tended to generalize to an extent unwarranted by the facts at his disposal.

Pascher (1938), while including the genus in the Xanthophyceae, ventures the opinion that there appear to be, within this alleged genus, species which are not, perhaps, generically related, and suggests that it may be advisable to separate the green and colourless species. Jane (1942) concluded that it was desirable to raise to generic rank Pascher's subgenus *Chytridiochloris* for the reception of the pigmented species, whilst retaining the name *Harpochytrium* for the colourless ones. The subsequent investigation of several species of *Harpochytrium* and of *Chytridiochloris viridis* (Scherffel) Jane (*Harpochytrium viride* Scherffel) has supported this view. *Chytridiochloris viridis* Jane (1944), with its oil and its uniflagellate zoospores, is unquestionably a xanthophycean alga, which is correctly placed by Pascher in the Heterococcinae (family Characiopsidaceae), and *C. Scherffelii*, as far as it is known, is sufficiently similar to justify generic association with *C. viridis*. Chromatophore apart, however, the resemblances between *Chytridiochloris* and *Harpochytrium* are superficial, viz. the tubular shape, the proliferating sporangia and the uniflagellate zoospore. Homoplasy may well afford a sufficient explanation of this similarity (Jane, 1942).

There are two outstanding differences between the two genera: (1) the uninucleate cells of *Chytridiochloris* as compared with the coenocytes of *Harpochytrium*, (2) the attachment of the zoospore by its anterior end in *Chytridiochloris* and by the tip of its flagellum in *Harpochytrium*; further, there is often a spherical basal vacuole in *Chytridiochloris viridis* which is not present in *Harpochytrium*, although at times there is a more irregularly shaped vacuole at the base of the cell in plants of the latter genus.

The inclusion of all the non-pigmented species in the one genus *Harpochytrium* seems justifiable: little information is available in regard to *H. apiculatum*, but its shape, proliferating sporangium and absence of pigmentation furnish reasons for its inclusion in the genus, at least for the present.

As to the systematic position of *Harpochytrium* there are two possibilities: either the plants are non-pigmented xanthophycean algae, or they are Phycomycetes, but not necessarily chytridiaceous. Apart from the absence of a rhizoidal system, there is little in *Harpochytrium* which points to xanthophycean affinities, and this feature alone scarcely excludes the genus from the fungi. It is true that the Chytridiales possess a rhizoidal system, but among the higher fungi some of the Laboulbeniales have a foot which develops no rhizoidal system and which scarcely penetrates the host—a holdfast, not a haustorium. Further, it is not possible to demonstrate in *Harpochytrium* certain characters shown by many of the Xanthophyceae, viz. a lamellate wall, a wall composed of two overlapping pieces and the presence of pectic substances: the absence of such characters, however, does not afford conclusive evidence of non-xanthophycean affinities (Pascher, 1938; Jane, 1944). Moreover, too much significance cannot be attached to the apparent lack of a lamellate wall in *Harpochytrium* owing to the extreme smallness of the plants and consequent difficulties of observation, while the presence of a wall composed of two pieces would be demonstrated only by a lid-like dehiscence of the sporangium, a feature not unknown in the Chytridiales.

At least two of the species of *Harpochytrium* are occasionally branched (Atkinson, 1904; Jane, 1942, 1946); admittedly this is a rare phenomenon, but it is indicative of a potentiality in the genus. With the exception of the peculiar *Trypanochloris*, there are no records of branching in any member of the Heterococcales. If *Harpochytrium* be a colourless alga, it should be assigned, it would seem, not to the Heterococcales, but to the Heterosiphonales.

Points of resemblance to the lower fungi are equally unsatisfying. The lack of pigment points towards the fungi, but non-pigmented algae are not unknown. Oil storage is no more a xanthophycean than a fungal character, while the zoospore characters are not decisive. Possibly the chitinous walls, present at least in *H. Hedinii*, indicate fungal affinities, but this is scarcely a criterion, since too little is known of the nature of the walls of either group. Chitin has been demonstrated in some of the lower fungi and not in the Xanthophyceae (van Wisselingh, 1925), but tests made during the present investigation gave a faint positive reaction in *Ophiocytium*.

It is extremely doubtful if *Harpochytrium* is a member of the Chytridiales (Rhizidiaceae); its zoospore characters alone militate against this view. The relatively large part of the plant which remains sterile, the apparently unlimited growth in length (Jane, 1946), the coenocytic habit, the potentiality for branching, and perhaps the potentiality for forming cellulin plugs (cf. Jane, 1946), are features which suggest affinities with the lower Oomycetes, although at present there is no evidence that *Harpochytrium* reproduces by sexual means.

It is thus evident that our present knowledge is insufficient to decide on the affinities of *Harpochytrium*, and that there is as much, or as little, to be said in favour of its algal affinities as its fungal ones. I am inclined to regard the plants as primitive or reduced non-chytridiaceous Phycomycetes, in which the small mycelium, with its high ratio of length to diameter, gives a maximum absorbing surface for nutrient materials present in very small concentrations in the relatively pure waters in which the plants live.

Taxonomy

Harpochytrium Lagerheim

Lagerheim (1890), Fischer (1892), Schröter (1897), Wille (1900), Atkinson (1903, 1904), von Minden (1915), Scherffel (1926), Printz (1927), Pascher (1938).

Syn. Fulminaria Gobi (1899); *Rhabdium* Dangeard (1903).

Classification. Harpochytriaceae (incertae sedis).

Saprophytes, normally epiphytic on living, freshwater (usually filamentous) algae, more rarely on dead organic remains and inorganic material: usually gregarious.

Plants normally unbranched, very occasionally branching. Cylindrical, straight or slightly to strongly curved, sometimes standing erect or obliquely erect to host filament, sometimes curving around or along it; apices rounded, bluntly or acutely pointed, or prolonged into a bristle; bases but slightly tapered and relatively undifferentiated, or strongly contracted into a thin stalk; basal end terminating in a foot, which is a holdfast; stalk short to long; foot usually fixed superficially to host, or even to the surface of its mucilage, sometimes by a pad of pectic ? mucilage; foot at times penetrating outer wall of host ?; foot and stalk basal, sometimes becoming displaced to a lateral position during development.

Cell wall very thin but thickened at base of cell; not visibly lamellate, nor composed of two unequal overlapping parts; devoid of cellulose; devoid of pectic substances except at times in foot and stalk; may contain chitin; shows marked affinity for congo red and trypan blue; resistant to cold concentrated sulphuric acid but not to 40 % chromic acid.

Plants coenocytic; uninucleate in young stages and usually immediately after spore formation; transverse septa very rarely formed. Cytoplasm usually finely granular; often containing some larger granules and a few large, or more numerous small globules of fat or fatty acid. Cytoplasm often vacuolate; vacuoles at times relatively large and numerous. Plants not pigmented.

Reproduction by swarmers, produced in a sporangium formed from distal end of cell; sporangium proliferating. Swarmers produced by transverse segmentation of protoplasm, and in broader plants by longitudinal segmentation as well? Contents of sporangium not separated from residual protoplasm by a transverse wall. Zoospores liberated from apex of sporangium; uniflagellate, more or less spherical, but strongly 'metabolic' and sometimes amoeboid; uninucleate; becoming attached to host plant by tip of flagellum.

Hypnospores, with stout wall and storing abundant fat, may be produced; this process rare in nature?

It is possible that the above generic description is over-generalized, but at present it seems desirable to err in this direction.

Key to the species of Harpochytrium

I. Plant without appreciable stalk.		
A. Plant adpressed to host.		
1. Plant strongly falcate.	*H. Hedinii*, f. *falcata.*	5
2. Plant somewhat curved but not strongly falcate.	*H. Hedinii*, f. *adpressa.*	5
B. Plant erect or sub-erect.		
1. Plant curved.		
a. Stalk and foot very small, plant sabre-shaped.	*H. Hedinii*, f. *Atkinsoniana.*	5
b. Stalk and foot stout, plant strongly curved.	*H. Botryococci.*	1
2. Plant straight, sometimes somewhat sinuous or slightly curved.		
a. Apex not terminating in a bristle.	*H. tenuissimum.*	2
*Apex bluntly pointed.	*H. tenuissimum*, f. *vera.*	2
** Apex acutely pointed.	*H. tenuissimum*, f. *elegans.*	2
b. Apex terminating in a bristle.	*H. apiculatum.*	3
II. Plant with a conspicuous stalk.		
A. Plant erect or sub-erect.		
1. Plant sabre-shaped, apex usually blunt.	*H. Hedinii*, f. *Atkinsoniana.*	5
2. Plant straight or slightly sinuous, apex acutely pointed.	*H. monae.*	4
B. Plant lying more or less parallel to host filament, or at least, not erect.		
1. Stalk short, expanding into foot.	*H. Hedinii*, f. *adpressa.*	5
2. Stalk long, not expanding into foot.	*H. Hyalothecae.*	6

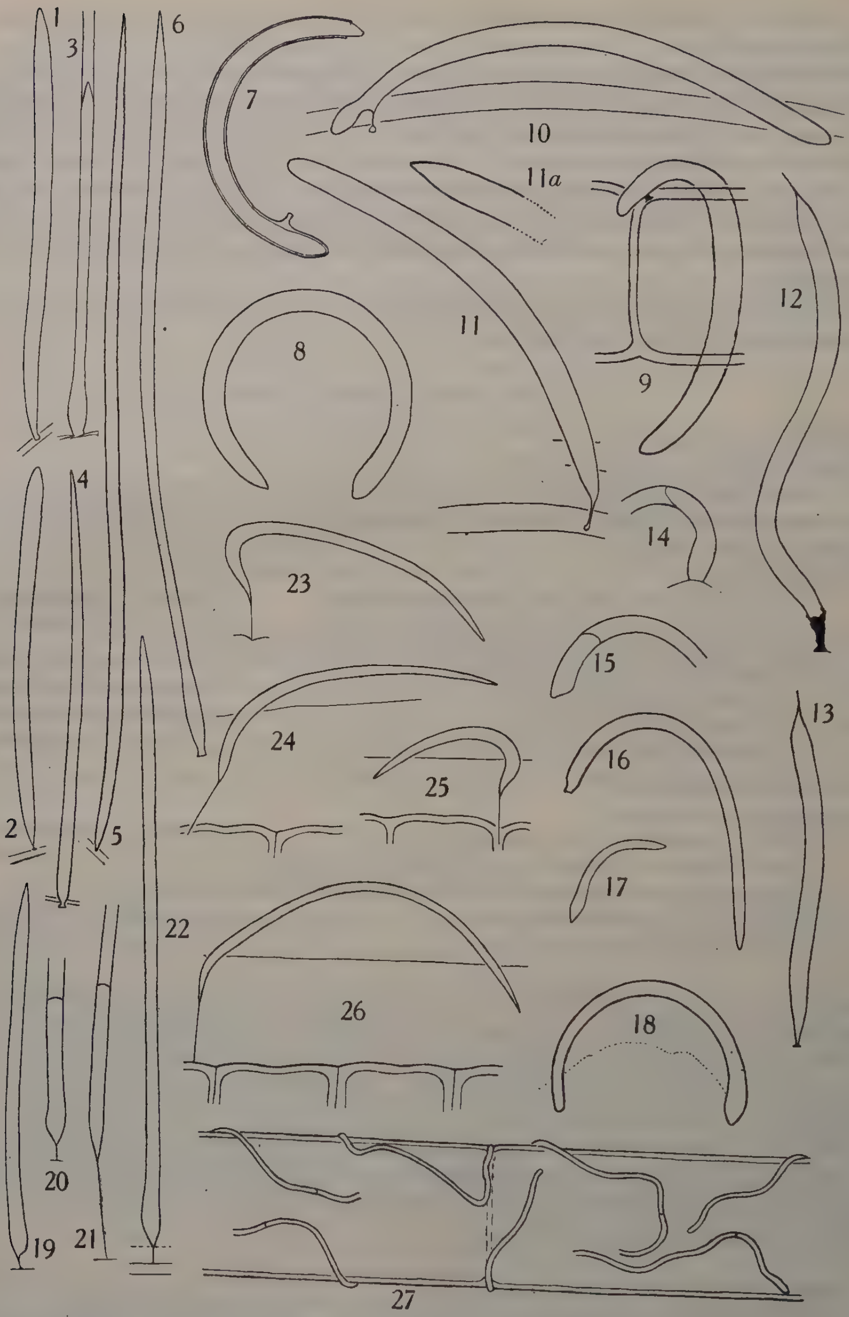
Apart from unusual growth forms such as have been found in *H. Hedinii* and *H. tenuissimum* (Jane, 1942, 1946), all the species of *Harpochytrium* which have been studied in the course of the present investigation are quite distinct; as far as may be judged, this applies to the species which I have not seen. In culture, however, there is considerable fluctuation in the dimensions of the cells; personal observations suggest that there is some variation in this respect in nature, and this view is strengthened by the dimensions which other authors have given. Notwithstanding their poor diagnostic value, dimensions of the species have been included in the descriptions of the species, and probably serve to give an indication of the range in size.

1. *H. Botryococci* sp.nov. (Figs. 14–18)

Plantae minutae, ad 50μ longae, $1{\cdot}2$–$2{\cdot}6\mu$ crassae, ex cellulis hospitis exstantes, plerumque valde curvatae, apice rotundatae rarius subacutae, basi attenuatae, interdum truncatae. Zoosporae paucae, ad 7–8 modo, e tribus duas partes cellulae occupantes.

Hab. in *Botryococco*, interdum mucilagine hospitis omnino immersae.

Plants minute, cylindrical, usually strongly curved; apex rounded, rarely somewhat acute; usually tapering to a point at the base; base sometimes truncated; very rarely with a stout, very short stalk and broad foot; cell sometimes swollen proximally and sometimes slightly tapered distally; cell sometimes forming transverse septa.



Figs. 1–27. Outline drawings of all the known species and forms of *Harpochytrium*; those of *H. apiculatum* and ? *H. vermiculare* after Pascher. All the drawings are to the same scale, except those of Pascher, which are *about* half the size of the others. As far as possible typical plants of all the species and forms have been selected, but there is much variation in shape and size in most of the species.

Figs. 1–6. *H. tenuissimum*. 1, 2, forma *vera*; 4–6, forma *elegans*.

Figs. 7–11. *H. Hedinii*. 7–9, forma *falcata*; 10, forma *adpressa*; 11, forma *Atkinsoniana*: the rounded apex shown in Fig. 11 is less typical than the more pointed one which is shown in Fig. 11*a*.

Figs. 12, 13. *H. apiculatum*.
Figs. 14–18. *H. Botryococci*.
Figs. 19–22. *H. monae*.
Figs. 23–26. *H. Hyalothecae*.
Fig. 27. *H.* ? *vermiculare*.

About two-thirds of the cell used in the formation of the sporangium. Zoospores few, probably not exceeding 7–8 per sporangium. Sporelings at first scarcely curved; with prominent basal swelling. Cells up to 50 μ long, 1·2–2·6 μ broad, except at basal swelling, where they are 1·9–2·8 μ in diameter.

Plants standing away from host cells; sometimes completely embedded in host mucilage.

On *Botryococcus*: Caernarvonshire; Llyn Bychan, 16 September 1933 (this material was preserved in formol; it was collected by Mr N. Woodhead); Llyn Crafnant, 14 September 1942.

On account of its small size and the deep orange mucilage of the host, this somewhat variable species is difficult to study. It is always curved, sometimes so much so that distal and proximal parts of the cell lie parallel; the swollen basal region is fairly characteristic, but does not occur invariably. It is the only species in which transverse walls, formed other than in relation to the sporangium, have been observed, but this is a rare occurrence. The attaching region seems to be variable, but it is not easy to study this part because of the deep colour of the host; some plants have a distinct, very short, stout stalk and a broad foot, others a truncated base, and, in some plants the proximal end of the cell is pointed, and the foot, if present, very small.

The cell contents resemble those of other species. In the scanty material available, nuclei could not be demonstrated conclusively; some clear vesicles which contained granules were observed in stained preparations and were probably nuclei; if so, the nuclei have a diameter of 0·7–1·0 μ and are about three to six per plant.

Escaping zoospores were not seen; segmenting sporangia indicate that few spores (up to eight ?) are produced by a sporangium.

2. *H. tenuissimum* Korsch. emend. Jane (Figs. 1–6 and 28)

H. tenuissimum (pro parte). Korschikoff (1931), Pascher (1938), Jane (1942).

Syn. H. intermedium (pro parte) Scherffel (1926), Pascher (1938), ? Atkinson (1903, 1904), ? von Minden (1915).

Icones. Scherffel (1926), Korschikoff (1931), Jane (1942), ? Atkinson (1903).

Cells more or less cylindrical, normally straight, rarely somewhat curved or sinuous, occasionally branching, or forking at apex. Cells often swollen at base, otherwise of even diameter until near apex, or sometimes tapering very gradually from base toward apex; more rarely cell tapers toward base; irregular swellings, apart from basal swelling, formed very occasionally. Apex rounded, obtusely or acutely pointed. Foot and stalk variable; stalk always stout and very short, usually expanding slightly, or considerably, into foot, which is sometimes surrounded by pectic ? mucilage.

Cell wall very thin, slightly thicker at base of cell. Nuclei generally few, 4–5 (9) per cell.

Zoospores few per sporangium (not exceeding about 12), more or less spherical, but changing shape; diameter exceeding that of plant from which they are liberated; with fine flagellum of diverse length. Sporeling variable, with or without distinct basal swelling; apex ranging from blunt to acute; uninucleate. Plants may pass into resting condition without change (akinetes).

Plants erect or standing somewhat obliquely to host.

Plants up to 200 μ long and up to 4 μ in diameter. Pascher (1938) gives length as over 100 μ and diameter as 4–6 μ.

(*a*) forma *vera*: cells with rounded or obtusely pointed apices; often with bulbous base; sporangia may be formed in short plants (not exceeding 30 μ in length).

(*b*) forma *elegans*: cells with acutely pointed apices, bulbous base not frequent; sporangia rarely produced in short plants (length usually exceeding 50 μ).

On various algae, especially *Oedogonium*, *Microspora* and *Geminella*.

Carpathians (Scherffel), Russia (Korschikoff), Czecho-Slovakia (Pascher), ? U.S.A. (Atkinson), ? Germany (von Minden); North Wales: Caernarvonshire, at Bangor, Criccieth, Glyder Fawr, Nant y Benglog, and Anglesey, at Llandegfan Common and Mynydd Bodafon.

This is a very variable species, with two extreme forms which were formerly considered as distinct species. The nomenclature is rather confusing. Atkinson (1903, 1904) described a *Harpochytrium* found on '*Conferva utriculosa*' at Ithaca as *H. intermedium*. Both von Minden (1915) and Scherffel (1926) accept this species, but Atkinson's description and figures appear to be too vague for the plant to be identified with any species subsequently described, or to enable the plant to be recognized again. It is therefore proposed to regard *Harpochytrium intermedium* as a *nomen nudum*. Korschikoff (1931) described, as a new species, plants which somewhat resembled those which Scherffel (1926) had described, and referred to Atkinson's species. Korschikoff's plants, which had obtusely and not acutely pointed apices, were named *H. tenuissimum*. Pascher (1938) suggested that Korschikoff's material might represent an extreme variant of those described by Scherffel (and Atkinson), but Jane (1942), describing plants which appeared to agree closely with Korschikoff's *H. tenuissimum*, then considered that these plants were distinct from those of Scherffel, especially in the shape of the apex. Subsequent examination of many plants from various localities, together with cultured specimens, showed that it was not possible to refer some plants to one or the other 'species'; the apices, which appeared to be the best diagnostic guide, varied much more than those of earlier collections of *H. tenuissimum*, and neither the bulbous base nor the shape of the stalk and foot appeared to furnish a reliable means of distinguishing between the two forms.

A study was made of the variation in apices and basal regions of plants selected at random from several collections and cultures. In each sample drawings were made of the first dozen plants in a position suitable for drawing; a selection of such plants is shown in Fig. 28 and it is apparent that the presumed difference between the two 'species' breaks down. The apices shown in row A are from plants from the locality in which *H. tenuissimum* was first collected (Jane, 1942); most are forma *vera*, although A1 resembles forma *elegans*. Row B again shows forma *vera* and is from a locality where the plants are predominantly of this form, just as those of row C are from a locality where forma *elegans* is nearly always found. The plants figured in row D are from the same locality as those of row C, but from a culture where, it is believed, fouling of the medium had occurred; the appearance of plants of forma *vera*, D1–7, is striking. Plants shown in row E are from the same locality as those shown in row B, but from an old, stale culture; the rounded apices of those shown in E1–6 are noteworthy. In row E it will be observed that both the *vera* and *elegans* forms occur. The figures demonstrate that the two forms cannot be regarded as other than growth forms. In regard to the base of the plant, this tends to be swollen more often in plants of forma *vera*, and it is also to be observed that sporelings from localities in which forma *vera* predominates more frequently show a bulbous base than those from predominantly forma *elegans* localities. Neither of these features is, however, so reliable a guide to identification as the apex.

Since Atkinson's name cannot be accepted, the species must be named *H. tenuissimum* Korsch. emend. Jane, and it is proposed to regard the extremes as forms, forma *vera* to include plants similar to those figured by Korschikoff (1931) and Jane (1942), and forma *elegans* for those similar to that figured by Scherffel (1926).

In this species the variation in length is enormous, and greater than that among any other species studied: the longer plants are to be found in old cultures, where, owing to staling, very favourable conditions for growth presumably arise.

With one exception, it is the only species in which branching occurs, but this is rare. *H. tenuissimum* is also remarkable for the large number of host plants and other substrata on which it is able to grow. Most of these, however, are seldom used, and in nature the species shows a decided preference for *Oedogonium*, *Microspora* and *Geminella*.

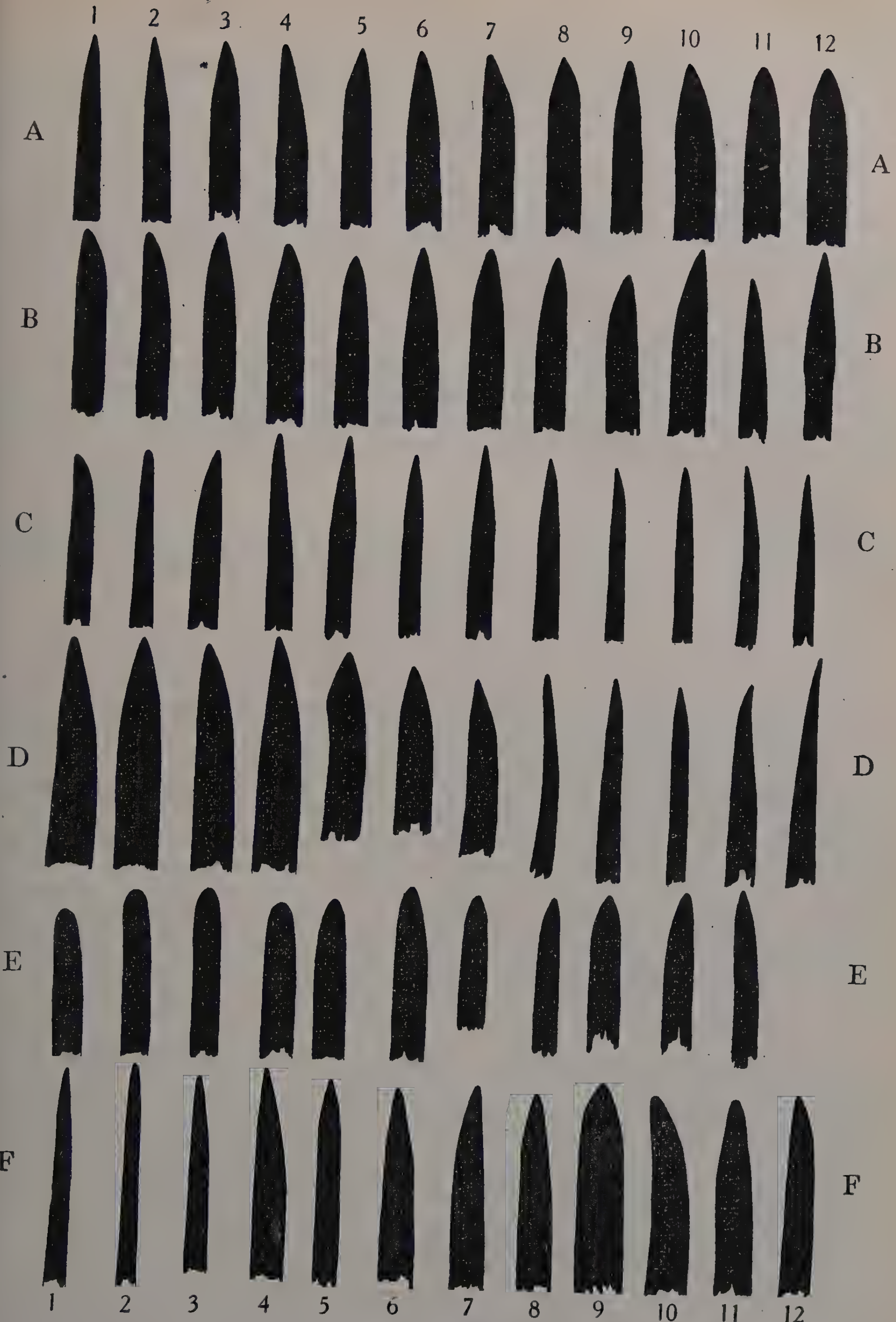


Fig. 28. Variation in the apex of *H. tenuissimum*: these apices are from plants from different localities and grown under different conditions; plants of each batch were selected at random. Row A. From grounds of University College of North Wales, Bangor, old culture. Row B. From Llandegfan Common, Anglesey. Row C. From Nant y Benglog, Capel Curig (a forma *elegans* locality), from culture in rain water. Row D. From the same collection as row C, but in an old hanging drop culture. Row E. Llandegfan Common, Anglesey, an old culture; compare with row B. Row F. From Mynydd Bodafon, Anglesey.

3. *H. apiculatum* Pascher (Figs. 12, 13)

Pascher (1938).

Icones. Pascher (1938).

Cells cylindrical, straight or somewhat sinuous; tapering, sometimes somewhat unequally, to base, base not infrequently covered with iron salts; a stalk is sometimes developed; apically, cells which have not proliferated are shortly and sometimes sharply pointed, and may be drawn out into a short bristle. Zoospores unknown. Young cells almost fusiform. In proliferating cells apical end may become rounded.

Cells 4–6 μ in diameter. Plants standing erect from host.

On *Microspora*; Riesengebirge.

A little known plant which can be regarded only provisionally as a *Harpochytrium* on account of its terminal proliferating sporangium and the absence of pigmentation. The very pointed apex, which is not seen in plants with proliferating sporangia, is of interest for it indicates that the growth of the cell is apical.

4. *H. monae* sp.nov. (Figs. 19–22)

Plantae cylindricae, erectae, raro leviter curvatae vel sinuatae, ad 80 μ longae, 2 μ diametro, apice acutae, basi plerumque incrassatae ad 2·6 μ, pedicellatae; pedicellus tenuis, longitudine variabilis, ad 14 μ, plerumque basi in pedem minutum inflatus. Cellulae dimidia pars in zoosporangium commutatur.

Hab. in *Zygnema*, rarissime in *Zygogonio ericetorum*, pedicello solum mucilagine immerso.

Plants cylindrical, straight or rarely slightly curved or sinuous; tapering gradually to an acute apex; base generally somewhat swollen, and contracting rather suddenly into a thin stalk which is of varying length, but always conspicuous; stalk usually expanding proximally into a minute foot.

About half of the cell is used up in the formation of the sporangium. Zoospores unknown. Sporeling at first variable in shape, ovoid, pyriform or broadly fusiform, later elongating into the form characteristic of the plant, and with prominent basal swelling. Cells up to 80 μ long, 2 μ in diameter, except at basal swelling where the diameter is up to 2·6 μ; stalk up to 14 μ long.

Plants standing erect from host cells, stalk alone penetrating mucilage sheath of host.

On *Zygnema* and very rarely on *Zygogonium ericetorum* in a temporary pool, Llandegfan Common, Anglesey; spring, 1943, 1944.

5. *H. Hedinii* Wille (Figs. 7–11)

Wille (1900), Atkinson (1903, 1904), von Minden (1915), Korschikoff (1924), Scherffel (1926), Graff (1928), Sparrow (1932), Pascher (1938).

Syn. H. Atkinsonianum Pascher (pro parte) (1938); *H. adpressum* Scherffel (pro parte) (1926), Pascher (1938); *Fulminaria Hedinii* Wille (1903); *Rhabdium acutum* Dangeard (1903).

Icones. Wille (1900), Atkinson (1903, 1904), Dangeard (1903), Korschikoff (1924), Scherffel (1926), Sparrow (1932).

Cells slightly or strongly curved, tapering both toward base and apex, or more or less cylindrical, with rounded base and rounded or tapered apex; apex obtusely or acutely pointed; stalk basal or lateral, rather short to very short, expanding into a very small foot, which perhaps at times partially penetrates wall of host; base may be blunt and peg-like, without expansion into foot (Sparrow, 1932). Cell without basal swelling.

Sporangium may (rarely) become displaced laterally by subsequent growth of the residual protoplasm. Zoospores sometimes numerous, sometimes produced in more than one row; at first amoeboid; uniflagellate; becoming attached to host by flagellum. Sporeling at first erect, either remaining so or growing along or around host cell; stalk and foot commonly becoming displaced to a lateral position by asymmetrical growth of basal part of cell.

Aplanospores containing numerous fat globules and with thick wall, may be formed (only in culture ?).

Residual protoplasm may form akinete ?

Plant standing erect or obliquely erect to host, or procumbent (more or less) upon it.

Length up to 130μ, diameter up to 5μ; but Pascher (1938) gives length as up to 150μ and diameter as up to 20μ or even more, while according to Atkinson (1904), a length of 180μ may be attained.

(*a*) forma *adpressum*: plant procumbent on host, over which it grows in any direction; base usually rounded, diameter of individual cell varying in different parts; stalk lateral.

(*b*) forma *Atkinsoniana*: plant erect or obliquely erect; not strongly curved; sabre-shaped; tapered toward base, which is somewhat pointed; stalk sometimes lateral, often terminal; diameter regular throughout cell.

(*c*) forma *falcata*: plant growing around or occasionally along host; strongly curved; rarely tapered toward base, which is usually rounded; stalk lateral; diameter regular throughout cell.

Chiefly on *Spirogyra* and *Zygnema*. Tibet (Wille), U.S.A. (Atkinson, Graff, Sparrow), Patagonia (Atkinson), France ? (Dangeard), Germany (von Minden), Russia (Korschikoff), Bohemia (Pascher), England, Leicester district (Jane, coll. Ingold).

Pascher notes that the trivial name is given wrongly by most authors as *Hedenii*; the species was named after Sven Hedin.

Pascher (1938) removed the erect forms described by Atkinson (1903) from this species to a new one which he has named *H. Atkinsonianum*. A careful study of the literature, as well as of abundant material sent to me by Professor C. T. Ingold, makes it apparent that such a rearrangement cannot be substantiated. Had Atkinson found only erect forms this course might have been justified, but he states that some of the plants curved round the host: moreover, Atkinson examined Hedin's Tibetan material, which, he was satisfied, agreed with his own American plants within specific limits; in Hedin's material he noted that erect and prostrate plants occurred, and it should be added that Wille (1900), in his original description of *H. Hedinii*, makes no mention as to the position of the plants in relation to the host. Atkinson (1903) figures what are to be regarded as true *H. Hedinii* and *H.* '*Atkinsonianum*' plants from this material. Similarly Dangeard's illustrations suggest that both erect and prostrate forms occur side by side, as does von Minden's figure, although in this the plants appear to be little more than sporelings. In the Leicester material most of the plants were curved around the host, but some of the plants proved to be mainly the form *adpressum*, with which were growing a number of the form *Atkinsoniana*.

Similarly, Scherffel's *H. adpressum* is less likely to be a distinct species than a form of *H. Hedinii*. It occurs on the same host as *H. Hedinii*, or at least, on one of the larger species of *Spirogyra*. The form *adpressa* of *H. Hedinii* which was specially frequent in some batches of the Leicester material, certainly bears a striking resemblance to that figured by Scherffel (1926). In both may be noted the varying diameter of the individual cells, the rounded base and the pointed apex. Unfortunately, our knowledge of the attaching organ in Scherffel's species is vague: in the form *adpressa* there is a rather short, laterally displaced stalk, ending in a foot, while the plant is slightly curved and lying along the host (Fig. 10). The plants do not lie in close contact with the host cell, although, seen from above, they appear so to do. While in forma *Atkinsoniana* the foot is usually terminal (invariably so in the plants examined by me), it may be laterally displaced (cf. Atkinson, 1903, pl. X, fig. 15). In forma *adpressa* and forma *falcata* I have seen only a lateral stalk and foot.

The peculiar stalk and foot, so often arising by asymmetrical growth of the sporeling, together with the fact that forma *Atkinsoniana* and forma *adpressa* occur on one and the same filament, and that the form *falcata* may be partially erect, appear to justify the inclusion of the three forms in the same species, and the limits set for *H. Hedinii* by the older authors are therefore followed.

H. Hedinii will, at times, grow on a small species of *Spirogyra*, although it shows a marked preference for one of the larger ones. It is on the small species that the form *falcata* is usually found, while forma *adpressa* and forma *Atkinsoniana* occur on the large one. The difference in the size of the host may be striking.

6. *H. Hyalothecae* Lagerheim (Figs. 23–26)

Lagerheim (1890), Fischer (1892), Schröter (1897), Atkinson (1903, 1904), von Minden (1915), Scherffel (1926).

Syn. Fulminaria gloeophila Gobi (1899), Wille (1903).

Icones. Lagerheim (1890), Gobi (1899), Scherffel (1926).

Cells more or less cylindrical, with a long, slender stalk which does not broaden proximally into a foot; cell not swollen basally, but tapering, usually asymmetrically, into the stalk; cell usually somewhat curved, often strongly so at base; cell sometimes twisted on itself; main part of cell usually lying approximately at right angles to stalk; apex acutely pointed, rarely rather bluntly pointed or even rounded.

Zoospore with single, long flagellum; said to move very rapidly; becoming attached to the host by flagellum. Sporeling with long stalk; at first more or less pyriform, soon elongating and becoming curved; rarely with basal swelling.

Plant up to 70μ long, up to 2μ broad, stalk up to 12μ long. Pascher gives dimensions as up to 40μ and up to 5μ in diameter.

Plant usually lying more or less along surface of host mucilage, but sometimes partially erect; stalk almost always at right angles (or nearly so) to surface of host.

On *Hyalotheca dissiliens*, which appears to be the favourite host: also recorded on *Sphaerozosma vertebratum*, *Cosmocladium*, *Dictyosphaerium* and palmelloid stages of various chlamydomonads.

Sweden (Lagerheim), Finland (Gobi), U.S.A. (Atkinson), Germany ? (von Minden): North Wales, Caernarvonshire, at Criccieth and Snowdon, Anglesey, at Llandegfan Common (Jane).

von Minden (1915) claims that this species is nearly related to, or perhaps identical with, *H. Hedinii*, but there seems to be no evidence to support this view. *H. Hyalothecae* is one of the most distinctive species of the genus, and among the hundreds of plants examined during the present investigation, not one has remotely approached *H. Hedinii* in form. Moreover, Atkinson was unable to infect *Spirogyra* with *H. Hyalothecae* or *Hyalotheca* with *H. Hedinii*. Pascher (1938) thinks it possible that *H. Hyalothecae* embraces several closely related species, but there appears to be no evidence to support this statement, either in the literature, or in the abundant Welsh material which I examined. There is some variation in shape, and to some extent in habit, but insufficient to justify even the establishment of forms.

Harpochytrium ? vermiculare (Fig. 27). Under this name Pascher (1938) briefly describes an organism which he discovered on a large *Spirogyra*. The plant is thin, cylindrical and almost thread-like, often curved and sinuous, the cells running over the host in all directions. There is a proliferating sporangium. The plants are $1{\cdot}5$–2μ in diameter, and 100μ or more long.

There is probably as much justification for the inclusion of this plant in the genus *Harpochytrium* as there is for the inclusion of *H. apiculatum*. The sinuous shape and relatively great length are, however, so different from what is seen in the known species of the genus, that it seems wise to adopt Pascher's cautious attitude in regard to this plant.

Are the species of Harpochytrium *distinct?*

It seems desirable to deal briefly with the question of whether the species of *Harpochytrium* are, in fact, species, or growth forms of the same plant, a question often asked during the course of this investigation.

While in two species, *H. tenuissimum* and *H. Hedinii*, several forms occur, a few observations will suffice to indicate that the evidence does not support the view that the species are mere growth forms.

In material from Llandegfan Common, Anglesey, three species of *Harpochytrium* were found in the same gatherings—*H. Hyalothecae* on *Hyalotheca*, *H. tenuissimum* chiefly on *Oedogonium* and *H. monae* on *Zygnema*. *Spirogyra* was present in these gatherings, as was *Botryococcus*, but there was no trace of either *H. Hedinii* or *H. Botryococci*. Similarly *H. Hyalothecae* was found on *Hyalotheca* at Criccieth, while *H. tenuissimum* occurred in the same gatherings, chiefly on *Oedogonium*, but there was no trace of *H. monae* on the abundant *Zygnema* in the dippings. Again, in material from Nant y Benglog *H. tenuissimum* was found, but not *H. Hyalothecae*, although *Hyalotheca* was abundant, nor *H. Botryococci* in spite of the presence of *Botryococcus*. With such facts available there seems no reason to question the distinctness of the species.

It may be added that Atkinson (1903) tried, without success, to infect *Hyalotheca* with *H. Hedinii* and *Spirogyra* with *H. Hyalothecae*.

My thanks are due to Professor C. T. Ingold for sending me several collections of *H. Hedinii* from the Leicester district, and to Dr M. Baecker, who collected the material on which *H. Botryococci* was first found. It is also a pleasure to acknowledge the generous assistance which I have received from Mr N. Woodhead, who introduced me to nearly all the localities from which I obtained material of *Harpochytrium*, and who has always been ready to supply me with any material containing *Harpochytrium* from his extensive collections of algal material from the North Wales area. I have also to thank Miss E. M. Wakefield, F.L.S. and Mr C. S. Chapman for translating my English descriptions of *H. Botryococci* and *H. monae* into Latin.

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How did the Sweet Potato reach Oceania? By JAMES HORNELL, F.L.S.

[With a sketch-map and 2 text-figures.]

[Read 25 October 1945]

Botanists are agreed that America is the area within which the sweet potato (*Ipomoea Batatas* Poir.) was first brought under cultivation. One consequence arising from this conclusion is that the problem of the means whereby it became diffused throughout the island world of Oceania has given rise to great controversy. Moreover, as it carried its Quichuan name (*kumar* or *kumal*) with it into Oceania, this heightens both the interest and the difficulty of ascertaining the particular agency responsible for its dissemination. Of the alternative explanations hitherto favoured, one affirms that this is an instance of diffusion to be attributed to the activities of old-time Polynesian explorers, who, sailing probably from Tahiti, voyaged eastwards, via Easter Island, in large double-canoes, and eventually reached some port on the Peruvian coast. It is presumed that these adventurers returned home after a sojourn in Peru sufficiently long to have enabled them to learn to appreciate the sweet potato as producing edible tubers of outstanding excellence. Carrying with them a supply of these tubers, together with their Quichuan name, it is inferred by Rivet (1928) and other fervent Americanists, that the wanderers succeeded in reaching the homeland in safety and in propagating there some of the marvellous tubers which they had brought from the South American coast.

The second hypothesis is put forward by Dr Georg Friederici (1929, 1936). He recognizes the many difficulties inherent in making a return voyage by way of Easter Island; he considers that the prevailing winds and currents on this route would make the voyage so prolonged as to render it difficult and even impossible to carry, within the limited capacity of a double-canoe, a supply of water and food sufficient in quantity to last over the first stage; further, without compass or chart and the knowledge of how to fix a position, how could a *single* vessel hope to make Easter Island? Whenever possible, it was the custom of Polynesian voyagers to travel in company as a fleet, with the individual vessels strung out in line abreast, in order to diminish the danger of missing their objective, often a low coral atoll, difficult to locate except at short range.

In Friederici's opinion the difficulties mentioned require the introduction of this tuber to have been effected by some other means. The only one which he considers satisfactory is to credit its introduction into Oceania to the colonizing activities of the Spanish explorers Mendaña and Quiros. These explorers undoubtedly did try to raise various crops on certain of the island groups which they discovered between 1568 and 1606—the Marquesas, Solomons, New Hebrides and the Santa Cruz Group, as detailed on a later page. Professor Roland Dixon (1932), however, while admitting that the Spaniards did introduce certain plants in this way, contends that Friederici's statement concerning the inclusion of the sweet potato in these introductions finds no direct confirmation when a critical examination is made of the contemporary records; he rejects Friederici's conclusion as an assumption unjustifiable on the evidence extant and one that rests solely upon negative and uncertain evidence.

As regards the various edible roots and tubers which were found in cultivation throughout Polynesia when Cook and other explorers visited this region in the eighteenth century, the consensus of opinion to-day is that if we omit the sweet potato, all others, such as the yams (*Dioscorea* spp.) and the taro (*Colocasia esculentum*), are of Indonesian or south-east Asian derivation. Even the coconut palm is generally considered now to be of the same origin (Merrill, 1920, pp. 377–8; Beccari, 1917) in spite of O. F. Cook's arguments (1901, 1910).

While willing to grant an Indonesian or Asiatic origin to these and certain other economic plants, Dixon finds himself unable to avoid the conclusion that this derivation cannot hold good for the diffusion in Oceania of the sweet potato. This belief is based mainly upon the fact that its name in the Quichuan language of the Lima region of coastal Peru —*kumar* or *kumal*—is used throughout Polynesia either in almost identical form or in some recognizable variation, as, for example, *kumara* in the Maori of New Zealand, and also in Raratonga, the Paumotus, Mangareva and Easter Island; *umara* and *umaa* in Tahiti; *kumala* in Tonga; *'umala* in Samoa; *uala* and *uwala* in Hawaii; with *kumaa* in the Marquesas and *ku'a'ra* in Mangaia.

Dixon fully recognizes all the difficulties involved in a voyage by Polynesians to South America and back, but he cannot see that any other explanation will account for the diffusion of the sweet potato, together with its Quichuan name, throughout Polynesia. He concludes that in spite of all the adverse conditions surrounding such an adventure, a return voyage between Polynesia and South America *must* have been achieved successfully at least on one occasion.

THE CHARACTER OF THE PREVAILING CURRENTS, DRIFTS AND WINDS IN THE PACIFIC OCEAN

Before entering upon a detailed consideration of the various means whereby the sweet potato and certain other plants of economic value may have been introduced into Polynesia and Melanesia, it is necessary to have a clear understanding of the bearing upon this problem of the normal interaction of the major drifts and currents present in the Pacific Ocean. Knowledge of the use to which these ocean currents may be put by navigators is also needed in order to throw light upon the feasibility or otherwise of Polynesian voyagers being able, not only to reach the South American coast, but also to set a correct course for home and to accomplish the return passage successfully.

It is unnecessary here to detail the causes which have as their effect the circulation of the *surface* water within this area. The first essential point we have to notice is that this surface circulation is reversed on the opposite sides of the equator. In the north the circulation is clockwise; after sweeping down the west coast of the United States, the cold California current veers to the westward, south of the twentieth parallel to form the North Equatorial Drift.

South of the equator, the circulation runs in a counter-clockwise manner; running northwards along the west coast of South America, a cold current, the Peru (or Humboldt) current turns north-westwards off the coast of Peru and Ecuador to form the South Equatorial Drift. This continues due west between the equator and the parallel of 15° south; as it approaches the eastern Polynesian island groups, it begins to throw off branches. Off the Marquesas Islands a southern branch diverges from the main stream, tending increasingly to follow a south-westerly course. This takes it through the northern Paumotus and thence through the Society Islands and the Cook Group where the obstruction caused by the many island groups hereabouts entails divergence towards the south-east. Eventually it is joined by the Australian current; then, under the influence of the westerly winds prevalent south of parallel 40° S., it turns eastwards to run straight across the Pacific towards Patagonia. Arrived off that coast, one branch rounds the Horn into the Atlantic, while the other or northern branch, after being reinforced by an upwelling of cold water, returns up the west coast of South America as the Peru current, with which we began this tale of the elliptical course of the surface waters of the South Pacific.

Winds. In the South Pacific Ocean, the trade wind, blowing from the south-east towards the equator, coupled with the westward trend of the South American coast in the Peruvian region, are the important factors which impel and propel the surface water running north along the coast of Peru and Ecuador into a current drift towards the north-west which is the beginning of the Southern Equatorial Drift.

Entries in many ships' logs record the onset of strong gales blowing up from the south-east in positions well out from the Peruvian coast, such as that noted in the log of the ship *Dagonar*, mentioned on a later page—a gale so violent that this vessel was thrown on her beam ends in October 1913. And it was mainly because of the steadiness of the favourable south-east trade wind that Magellan's pioneering course across the Pacific approximated to a direction west-north-west, a route which took his ships through the wide and almost island-free passage between the Paumotu Archipelago and the Marquesas Group, thereby preventing him from having opportunity to discover any of the island groups in Central Polynesia.

CONSIDERATION OF THE RIVAL HYPOTHESES

HYPOTHESIS A. *Importation from Peru by Polynesian voyagers*

Of the two strongest objections to acceptance of this hypothesis, one (*a*), the lesser, is that which emphasizes the great distance to be traversed on any voyage from Polynesia to Peru—some 2200 nautical miles by the shortest route which is that from Easter Island, the last Polynesian outpost on the east, while (*b*), the greater and more cogent, stresses the immense difficulties that would confront any voyagers who might contemplate making the return crossing when the time came to select and pursue successfully a homeward-bound course.

Before discussing these objections, it is necessary to emphasize that the present use of the term 'voyagers' is definite and precise, being limited specifically to adventurers who undertook voyages with a settled object or destination; in this instance it connotes those Polynesians who desired to make the return trip to the homeland after having succeeded in landing at some point on the western coast of South America. The outward journey may have been inspired by the urge to discover a new and happier country than their own circumscribed island, where, too often, the land consists of a narrow ring of coral rock, without adequate water supply and unresponsive to cultivation apart from that of the coconut. Or it may have been from sheer love of adventure and the desire to widen the horizon of their life. Whatever the cause, the voyages here referred to exclude those haphazard and unintentional ones which happen when vessels are driven off their course by storms. On these occasions people so driven forward, helpless and against their will, are to be considered as 'castaways' and lose the right to be considered as 'voyagers'.

This important distinction being made clear, we are in a position to consider the objections to the suggestions that have been advanced that Polynesians may have reached, on one occasion at least, that part of the west coast of South America where *Ipomoea Batatas* is cultivated under the name *kumar* or *kumal*.

With the knowledge obtained after careful analysis of the many traditional accounts of long voyages successfully undertaken by Polynesians between the tenth and fourteenth centuries (Smith, 1921; Best, 1923; Fornander, 1878), there can be no doubt that this people produced a succession of hardy adventurers during this period who sailed to and fro over the length and breadth of the Pacific. Guided in the first instance by the seasonal flights of migratory birds (Cartwright, 1929, p. 109), voyages between Hawaii and Tahiti, probably via the Marquesas and Fanning Island, were accomplished, involving a distance of more than 2400 miles. So, too, were voyages made in far-off days between Tahiti and New Zealand; even the names of many of the leaders are known, together with the fanciful names of the double-canoes in which they sailed. Distant Easter Island was occasionally visited—a far more hazardous journey because of the small size and lonely situation of the island, hundreds of miles beyond the eastern limit of the closely set island groups of central and eastern Polynesia (Smith, 1921; Thomson, 1889). Hazardous as this enterprise was, its perils were reduced considerably by the fact that there are several islands on the route where the voyagers could rest and reprovision;

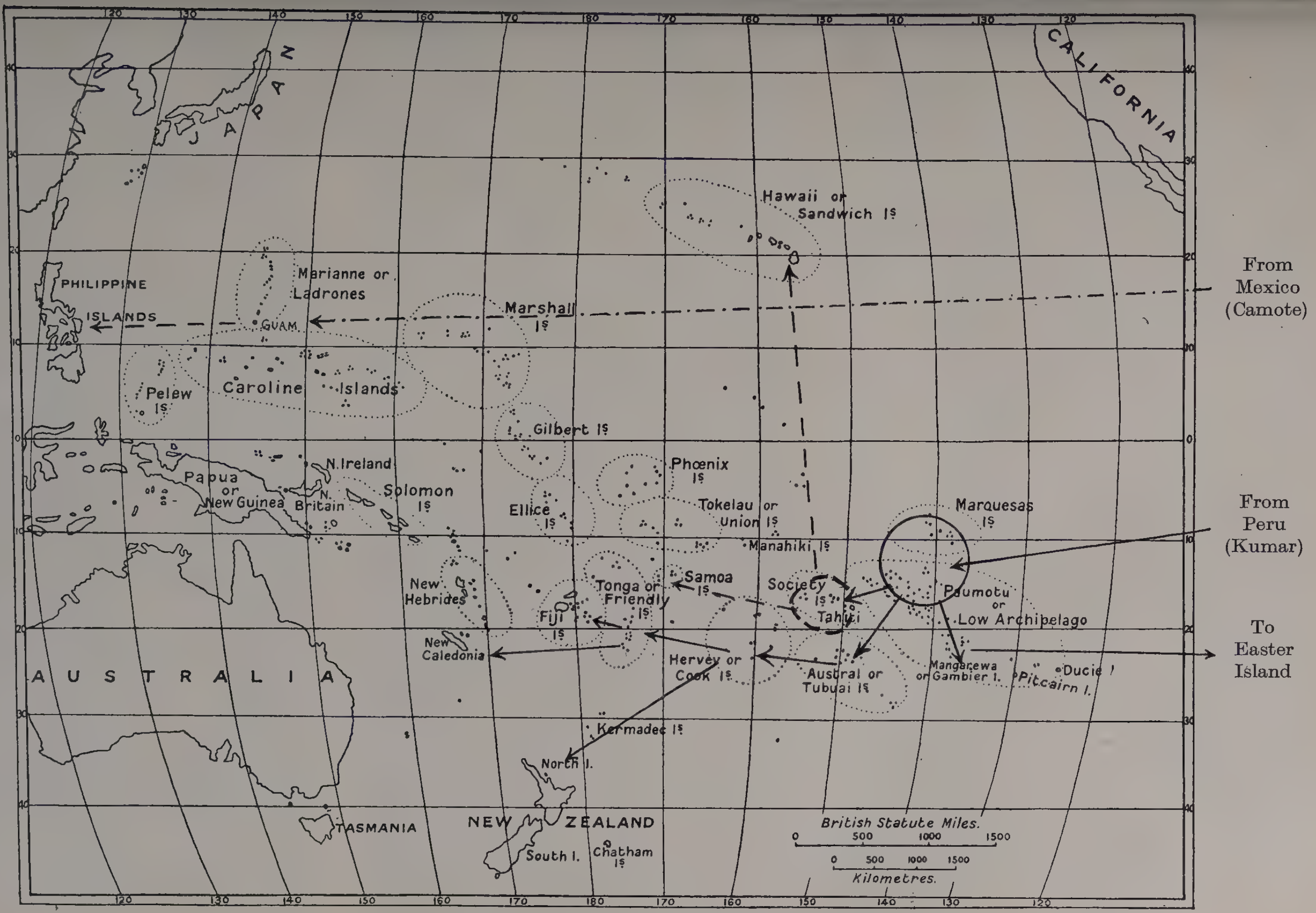
if they sailed from Tahiti, they had the choice of Rapa, Mangareva, Pitcairn and Ducie Island as intermediate stations on their route.

With these voyages to their credit, one to the coast of South America was well within the power of hardy adventurers manning a well-found and well-provisioned double-canoe of adequate size. If they went via Easter Island, they would experience no unsurmountable difficulties during a voyage which would take them to the Peruvian coast if the supply of food and water did not fail. Striking east or north-east from Easter Island, they would be bound to come within the influence of the Peru Current sweeping north, parallel with the Chilean and Peruvian coasts; they would find it a most helpful factor in making a landfall on the coast of northern Peru or of Ecuador.

Great and well-nigh insuperable difficulties would surround the successful accomplishment of any attempt to return home. Several vitally important initial difficulties would have to be overcome; the active goodwill of the Peruvian authorities and people would have to be secured—an uncertain quantity. Even more difficult would it be to determine what course to set on leaving the Peruvian coast. To return by the same route as that by which they had come would be to court disaster. As Dixon says (1934, p. 174): 'It is one thing to sail eastward and strike a continent, and quite a different one to sail thence westward and find again a single island.' Difficult as it would be to locate a lonely island without the aid of an accurate chart and modern navigational instruments, the plight of a Polynesian vessel, *sailing alone*, would indeed be desperate without such help, were the course unfamiliar and with wind and current adverse as they would be if the Easter Island route were attempted; on this course the voyagers would have to battle with the strongly running Peru Current; the westerly winds prevalent in the South Pacific would also impede return by this route.

It is obvious that a different course would have to be set if a successful return journey were to be made in a clumsy craft with a rig ill-adapted to contend with head winds and contrary currents. And how were Polynesian sailors to become possessed of such knowledge in unfamiliar waters? Out of their experience they could not obtain it, but this might be made good by information received from some of the Peruvian balsa sailors who may be credited with having had sufficient acquaintance with the run of the local oceanic current as to be able to indicate to the strangers that the northward-running coastal current—the Peru Current—veers towards the north-west in the latitude of northern Peru. Also, it may well be that the balsa sailors had some notion, actual or legendary, of the existence of the Galapagos Islands, just as Columbus and the early Irish had vague ideas of a land lying far out in the western Atlantic (Hornell, 1938, sec. 4, p. 75); if so, any reference to a group of islands lying far away in a north-westerly or a westerly direction would be liable to give the Polynesian visitors the mistaken impression that the reference was to the existence of some of their own Polynesian islands, marooned far out in the ocean. As a natural consequence this information would tend to sway their decision in favour of a return route on a course identical with the run of the current indicated by their Peruvian friends. Their own specific knowledge of the far-stretching arc of islands thickly strewn along the eastern fringe of Polynesia would reinforce further a decision to set a north-westerly course; their most experienced navigator may have considered that the chance of sighting one of these islands was sufficiently promising to justify the hazard to be incurred.

If this assumption were acted upon and if the run of the current indicated—the South Equatorial Drift—were followed, we are able to infer from our present knowledge of the direction taken by the currents and drifts of the South Pacific Ocean and of the help that would be received from the south-east trade wind in this part of the world, that such a course would take them close to or even through the Marquesas Islands; this probability will be demonstrated on a later page from the experiences of the drift voyages of derelicts and shipwrecked crews in this region within the present century, together with the evidence afforded by drift-bottle experiments.



Explanation of the Diffusion Routes
—·—·— Camote line, from Mexico,
———— Kumara line, from Peru,
— — — Umara line, from Tahiti.

If the returning voyagers had any sweet potatoes left uneaten on arrival at some Marquesan island, they would probably be given to the Marquesan people if the reception were friendly or taken from them if it were not, in the latter case without the Peruvian name. This alternative is improbable, for it fails to account for the presence of this name in the Polynesian languages and dialects.

There is, nevertheless, a way whereby the Peruvian term may have passed into the Marquesan vocabulary even were the reception hostile. We know that it was a recognized and salutary Polynesian custom when setting out on any lengthy voyage to provision their vessels with a variety of useful plants, fruits and domestic animals, in order to guard against the danger of stranding on an island bare of these necessaries. Their precautions against this danger sometimes went so far as to take aboard at least one woman and a sow with pig, to make sure of the permanent existence of the new settlement if so marooned (Best, 1923, p. 34). Special care would be exercised in the provisioning of a vessel for any attempt to return to the homeland from America. If one or two women were included in the lading, and if one of the outer Polynesian islands were eventually reached, it is reasonable to infer that the women would be spared, even if all the men were killed. On the advice of the woman or women spared, any tubers remaining aboard would be taken ashore and planted and its Peruvian name of *kumar* or *kumal* introduced into the island language in some modified form consonant with the local dialectic peculiarities of the island's speech.

If the wanderers had the misfortune to miss one of the Marquesan islands, they would have a chance of sighting one of the islands in the northern Paumotus or one or other of the mountainous islands, visible from afar, of the Society Islands, provided that they had determination to continue to follow the run of the drift which prevails in this region.

Such a sequence of happenings as I have envisaged may well be admitted as a possibility for men of the hardy and adventurous spirit of the ancient Polynesians, wise in their knowledge of the many successful endings to other hazardous enterprises, but we can hardly contend that it would have any considerable probability of achievement. All the same, when, as we know for certain, the Polynesians were able to sail backwards and forwards between Hawaii and Tahiti, and to find New Zealand and many other isolated islands, without charts or previous information concerning their presence or position, the difficulties besetting belief in the success of a return voyage from Peru to Polynesia tend to diminish greatly. Even so, it is obvious that to make an island landfall in the Pacific without chart, nautical instruments or sailing directions, is a gambler's throw, with the dice loaded against the voyager; examples of this are seen in the paucity of island landfalls made by the early European voyagers across the Pacific, notably by Magellan on his way to the Philippines and by Mendaña before reaching the Solomons.

HYPOTHESIS B. *The alleged Spanish introduction of the sweet potato*

Friederici (1929, 1936) is the most important of those who have sought to consider the allusions to the planting of various vegetable products in the Marquesas Islands and in certain Melanesian localities by the early Spanish explorers of the Pacific as offering a reasonable explanation of the problems of whence, when and how the sweet potato reached Oceania.

That there was no inherent or unsurmountable obstacle to this having taken place is admitted. The viability of sweet potato tubers is sufficient to permit them to remain in good planting condition under favourable circumstances of transit by sailing ship from America to the Pacific islands; we know that the Spaniards did introduce this plant into the Philippines from their American colonies, and that theirs was the agency which carried its seed tubers across the Atlantic from Hispaniola and successfully introduced it into Spain in the early part of the sixteenth century. Oviedo, who had seen it under cultivation in San Domingo (Hispaniola), writing in 1526, states that he introduced it himself at Avila in Spain (Ramusio's translation, III, pt. 3).

Within Oceania it must have been carried in viable condition over long distances by Polynesians sailing in double-canoes, for there can be no doubt that Hawaii received this plant either from the Marquesas or the Society Islands. Similarly, the sweet potato must have reached New Zealand from Tahiti or from the Cook Islands by means of sailing craft manned by Polynesians, seeing that it was found in New Zealand by Cook, Banks and others. From a common centre it must have reached Easter Island, for Roggeveen (1911, p. 125) found it a staple food of the islanders in 1722.

Unfortunately for the argument that the original introduction of the sweet potato into the Pacific Islands is due to Spanish activities, there is not a single definite reference to confirm this in any of the accounts which we have of early Spanish exploration in that area; as a consequence the supporters of this theory fall back upon 'probabilities'.

The facts so far as they are ascertainable are these:

(1) *Marquesas Islands.* In 1595, Mendaña discovered this group; he stayed about a week at Tahuata (Santa Cristina). There he is recorded to have sown maize (Quiros, 1904, I, 23). No mention is made of any other product having been sown or planted; it is as rash as it is unjustifiable for Friederici to assume that the sweet potato was among the problematical 'others' which he infers were introduced, seeing that he has no better reasons to offer than (*a*) the important food value of this tuber in the economy of the Peruvian Indians, (*b*) the customary practice of Spanish explorers of introducing useful plants into whatever new lands they occupied or intended to colonize, together with (*c*) the probability that its occurrence in the Marquesas was overlooked when the islands were rediscovered by Cook in 1775, although we learn that the tuber was in common cultivation there when the islands were visited by Marchand in 1791 (1798–1800, I, 71).

The only plants mentioned by Mendaña's chronicler as noticed on the Marquesas Islands are the coconut palm, giant bread-fruit trees, the graceful plantain or banana, plots of feathery sugar-cane and a few others. All those recorded are of Indonesian or of Asiatic origin, and conspicuous either because of their large size or from some peculiarity of habit.

Now, although we have Marchand's definite statement of the presence of the sweet potato in the Marquesas in 1791, neither Cook, nor Forster, nor Porter, nor anyone else who visited these islands towards the end of the eighteenth century, and during the opening decades of the nineteenth, makes reference to its occurrence there; this suggests that, though it may have been present at that period, it was not of sufficient importance to arrest the attention of the casual observer. In any case the omission by Cook and others to make specific mention of the sweet potato as grown here is not conclusive evidence of absence; in particular, Cook's reference is too vague to convey any certainty of identification.

(2) *The Solomon Islands.* These islands were discovered in 1568 by Mendaña in the course of his first voyage westwards. Again, there lacks any mention of the sweet potato having been seen in cultivation anywhere. Neither is there any record of seed having been sown nor of the planting of new economic products, although it is probable that something of this kind was done in view of the prolonged stay, extending over several months, made by the expedition.

(3) *The Santa Cruz group.* The initial success of Mendaña's first exploring voyage led to a second, during which this group was reached in 1595. Here, if anywhere, we ought to hear of the planting of the sweet potato, for the Spaniards made a tragically unsuccessful attempt to colonize the principal island, Santa Cruz (Nitendi). During their stay there of three months sowing and planting were contemplated, and some must surely have taken place, but no record of this is to be found in the account given by the chief pilot, Quiros; he does, however, make mention of 'one, two or three roots like sweet potatoes, in use by the natives' (1904, I, p. 154).

(4) *The New Hebrides and the Marianas.* The records of Quiros's discovery in 1606 of the island of Espiritu Santo in the New Hebrides and those of Pigafetta concerning Magellan's stay at Guam (or at Rota) in the Mariana or Ladrones Islands in 1521, furnish weighty historical evidence favouring belief in the pre-Columbian presence of the sweet potato in eastern Melanesia.

As to the New Hebrides, both De Leza (Quiros, 1904, p. 376) and Torquemada (1723, v, cap. 69), in their respective accounts of Quiros's expedition, record the occurrence on Espiritu Santo of the sweet potato, the former by the Mexican name *camote*, and the latter by the Antillean name of *batata*,[1] both terms in use at that time to distinguish the sweet potato from *Solanum* potatoes (*S. tuberosum*) which they called *papas*. These definite identifications appear adequate as furnishing presumptive evidence that the sweet potato was under cultivation in Melanesia before the first known contact with Spanish voyagers from South America.

Torquemada (1723) adds the extraordinary statement that ordinary potatoes were also brought by the natives, distinguishing them by using the term *batata* for *Ipomoea Batatas* and *papas* for potatoes of the ordinary kind (*Solanum* sp.).

Further, there is a note in the legend attached to the chart of the Bay of St Philip and St James, Espiritu Santo, the work of Diego de Prado y Tobar, that the food of the natives 'consists of yams, potatoes (*papas*), plantains, coconuts, oranges and some figs' (Quiros, 1904, p. 471).

These statements of the presence of the *Solanum* potato in the New Hebrides at the time of Quiros's visit appear to be due either to verbal laxity or to confusion in the recording; otherwise why should Quiros have included *Solanum* potatoes in his planting at the time when he attempted to form a settlement during his stay there of thirty-nine days, if they existed there already, as De Leza has recorded? According to his account (Quiros, 1904, p. 387), the General, wishing to provide the prospective settlers with adequate supplies of fruits and vegetables after the departure of the ships, and 'seeing that the land is so good and that it can raise any seeds that are sown in it, went on shore and went to their [the natives'] farms to sow calabashes of Peru, maize, melons, potatoes and peas, besides other seeds which I do not mention; for there were none of us who would not do his part in sowing like those who desired to settle'.

The potatoes thus planted were undoubtedly those of some species of *Solanum*, for the word used in the Spanish text is *papas*, the usual Spanish term for the common potato as has already been noted; it is most unlikely, however, that these *papas* tubers became established. We never hear again of their presence in the New Hebrides, where the hot, humid climate would be unfavourable to their growth.

Regarding the Marianas, the evidence that *Ipomoea Batatas* was already established there in the early part of the sixteenth century is less equivocal. Pigafetta, in his account of Magellan's voyage across the Pacific in 1520–21 (1874, p. 70), says of the island (Guam or Rota) off which Magellan anchored on 6 March 1521: 'Their provisions are certain fruits called Cochi [coconuts] and Batate: there are birds, figs a span long [bananas or plantains], sweet canes and flying fish.' At that time *I. Batatas* had already been introduced into Spain under the name *batata*, a word which eventually became naturalized in the Spanish language; in any case it seems reasonable to believe in the accuracy of Pigafetta's identification, for he had already recorded (1874, p. 43) the *batate* as among the provisions taken aboard the *Victoria* at a port in Brazil during the early part of 1520; he must therefore have been well acquainted with its appearance. The use of the Antillean term at a Brazilian port would accord with local linguistic requirements—both the Arawaks and the Caribs reached the Antilles from the north coast of South America.

But, if we are to accept Pigafetta's statement at its face value, we have then to account for the present Guam name, *kamote* or *kamute*, for the sweet potato being derived from the Nahua (Mexican) term *camotl* (corrupted in Spanish into *camote*) and not from the Antillean *batata* or the Quichuan *kumar*; this means that the current Guam name must have been introduced, ousting any previous name, at that later period when Spanish intercourse between the Philippines and Marianas and the Mexican port of Acapulco had become a dominant factor in the affairs of the island colonies of Spain in the western Pacific.

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[1] From this it will be noted that the plural form 'batatas', incorporated in the scientific name, is erroneously employed; Poiret ought to have used the form *Ipomoea Batata*, but the original spelling must stand.

This introduction, or rather reintroduction, probably took place during the century subsequent to 1662, for we know from Safford (1903) that Jesuit missionaries were active during this period in promoting the cultivation of the sweet potato by the people of Guam. It appears probable that this intervention led to the adoption of the Mexican term in the form *kamote* when we learn that this tuber was grown in Guam mainly for supply to passing ships coming mostly from Mexican ports, whose crews, short of fresh vegetables, would ask for the sweet potato by this name. Even so late as 1828, Villalobos was encouraging its cultivation for the same purpose.

Safford adds that the Guam natives never considered the sweet potato as a staple food, preferring yams and taro.

Pigafetta's record of the sweet potato as established in Micronesia (the Marianas) in 1521, and those of De Leza and Torquemada of its presence in Melanesia (the New Hebrides) in 1606, are clearly indicative of very early transmission from the homeland in America. This does not necessarily mean that the transmission was direct; it is probable that these observations indicate a gradual spread or diffusion from one or other of the central or of the eastern Polynesian islands, usually by trading voyages from island to island and group to group; in consequence, its speed of spread would be very variable; rapid in regions or groups where intercommunication was frequent; slow where racial differences tended to keep the peoples apart, though even there the spread might sometimes be rapid as a consequence of raiding and looting expeditions.

Besides the specific references to the sweet potato above quoted, there is frequent mention by Spanish explorers of 'yams' being noticed in use at various other islands; it s therefore worth pointing out, when assessing the value of old Spanish records relating to the cultivation of the sweet potato in newly discovered lands, that the writers were not botanists and that the terms *inhame* and *ñiame* (and in translations the word 'yam') were often used loosely to signify any kind of large starchy tuber found in the tropics (Burkill, 1938, p. 95), instead of being restricted to the true yams (*Dioscorea* spp.). For example, Burkill has pointed out that L'Obel and Pena in 1570 figured *Ipomoea Batatas* under the name *igname*, and that Chabraeus in 1677 used *inhame* or *igname* for the same plant (Burkill, 1938, pp. 92 and 94).

This criticism also applies *pari passu* to some extent to the degree of credence to be given to Spanish references to the presence of the sweet potato in western Oceania. Some doubt must still remain even when the statements would appear decisive, as when they profess to attest the presence of *camotes* and *batatas* in certain groups.

HYPOTHESIS C. *The Hypothesis that the sweet potato was introduced into Oceania by voyagers from South America in pre-Columbian times*

This hypothesis was mentioned and summarily rejected by Dixon (1932, p. 40) as the only possible alternative, if we are to eliminate the Spaniards as the introducers of the sweet potato into Polynesia and Melanesia, and if we refuse to believe in the possibility of Polynesian voyagers sailing to the Peruvian coast in pre-Columbian times and then returning home with a quantity of tubers of this plant which were then cultivated there, with subsequent diffusion throughout Oceania.

Dixon's rejection of the hypothesis named was due to his assumption that 'we have no evidence that at any time the Indians of the Pacific Coast of South America where the sweet potato was grown, had either the craft or the skill for making long sea journeys' 1934, p. 174).

Little attention has been bestowed upon this idea, due (1) partly to reasoning similar to that given by Dixon, and (2) partly to the belief that balsa logs (of which the ancient Peruvian vessels were built) remain buoyant for a very limited time when immersed in water. Too much importance has, in my belief, been given to these objections.

Regarding the supposed lack of maritime initiative and skill of Peruvian sailors in pre-Columbian times, we should assume a cautious attitude. We know that the Spanish *conquistadores*, when sailing south from Panama, were greatly surprised to meet great rafts rigged with large square sails, sailing along the coast. Juan de Samanos (1842), writing in 1526, described one captured by Bartolomeo Ruiz, Pizarro's pilot, as big enough to have a burden of about 30 tons; it was built up in two tiers, the lower of thick and buoyant logs, the upper, which formed a kind of platform, formed of bundles of slender canes, upon which the passengers and cargo were placed, to keep them dry from the water that swirled up through the lower tier of logs. 'It carried masts and yards of very fine timber and cotton sails of proportionate size after the manner of our own ships and very good rigging of hennequen, which I say is like hemp, and some mooring stones [killicks] for anchors'. The mast was a bipod structure such as is used on Burmese rice-boats, and is closely related to the masts of Indonesian vessels of the present day.

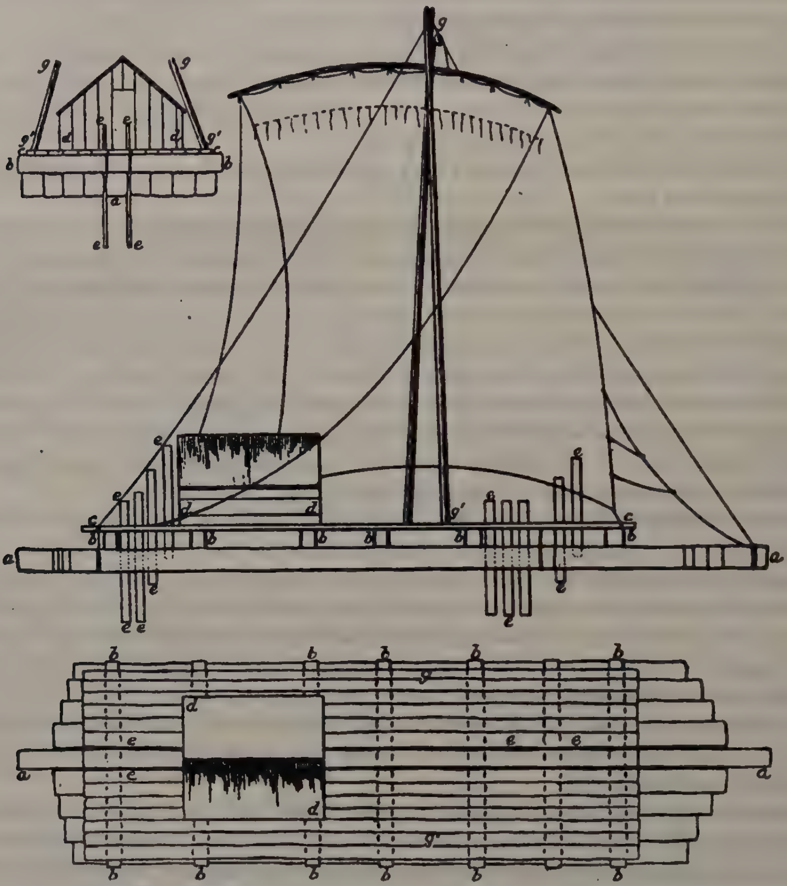

Fig. 1. Balsa-log raft, Guayaquil (*after* F. E. Paris). *a*, raft; *b*, cross beams; *c*, deck; *d*, cabin; *e*, centre boards; *gg'* mast sheers.

Juan and Ulloa, who visited Ecuador in 1736, state (1760, I, 189–92) that these sailing balsas made voyages from Guayaquil, carrying cargo to Puna, Tumbez and even to Paita in northern Peru. The authors named describe these vessels as 'composed of five, seven or nine beams of a soft wood, which, though known here only by the name of Balza, the Indians of Darien call Puero....The Balza is a whitish, soft wood, and so light that a boy can easily carry a log of three or four yards in length and a foot in diameter. Yet of this wood is formed the Jangadas or Balzas....Over part of it is a strong tilt, formed of reeds. Instead of a mast, the sail is hoisted on two poles or sheers of mangrove wood, and those which carry a foresail have two other poles erected in the same manner....The beams are fastened or lashed together by Bejucos, and so securely that with the cross-pieces at each end, which are also lashed with all possible strength, they resist the rapidity of the currents in their voyages to the coast of Tumbez and Paita. The Indians are so skilful in securing them that they never loosen, notwithstanding the continual agitation....' [Fig. 1, after Paris, is the best representation we have of this type of craft.]

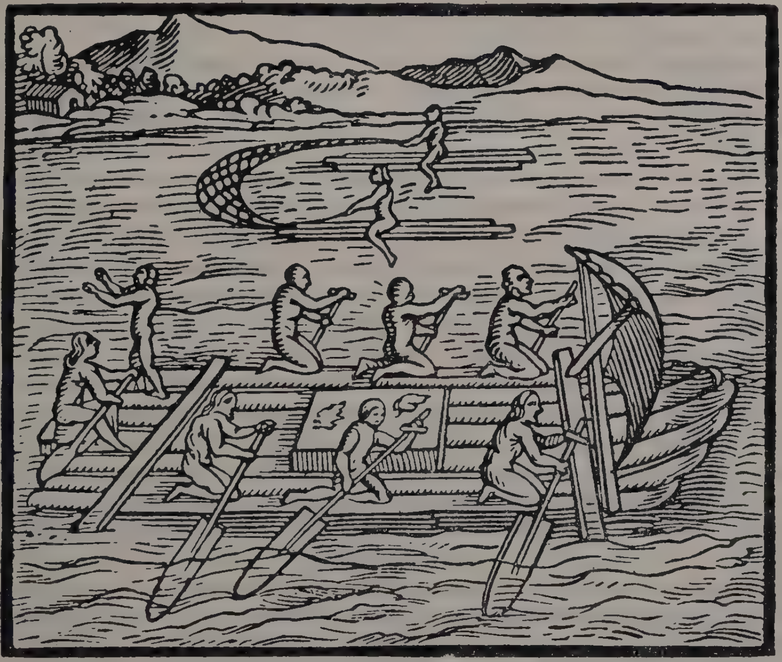

Fig. 2. Balsa of the Ecuadorian coast and of the north of Peru. (From an old print by Benzoni, dated 1565.)

'The larger sort of Balzas generally carry between four and five hundred quintals without being damaged by the proximity of the water; for the waves never run over the Balza....'

These authors go on to say that 'the greatest peculiarity of this floating vehicle is that it sails, tacks and works as well in contrary winds as ships with a keel, and makes very little leeway'.

This last-mentioned ability was due to the use of a series of boards let down vertically through slots between the logs; these functioned as leeboards and centre-boards; it is said that the Indian sailors were so adept at manipulating these boards that a correct course could be kept under all but the most exceptional circumstances; these 'leeboards' were fitted both towards the head and the stern; five or six might be in use at the same time.

Size. These sea-going balsas are stated by Juan and Ulloa to have been made up generally of nine beams, 12–13 toises [about 1 metre to the toise] in length, each beam about 2 ft. or more in diameter, thereby giving it the approximate dimensions of some 23–25 ft. in length by a beam of nearly 20 ft. Both these authors and Benzoni give illustrations of this type of craft. That by Benzoni, rude in drawing, has the appearance of being an inshore vessel (Fig. 2), being without shelter, whereas that of Juan and Ulloa has a very serviceable square mainsail together with a sail set on a spar which we may consider to be a crude form of jibboom. On the hull platform, abaft the mast, is a thatched shelter cabin; near the stern is a square fire-box. To keep cargo and passengers dry, the middle region of the basal platform carries an upper platform erected upon stout cross-beams, and it is over this that the thatched roof is erected.

In vessels of this kind, provided the logs do not become sodden and waterlogged, quite lengthy voyages are feasible, even to the islands of Polynesia. Ample supplies of food and water could be carried comfortably, sufficient for a prolonged period; the set of the Peruvian current was certainly known and Peruvian sailors probably had some knowledge of the alteration in its course towards the north-west as it approaches nearer to the equator. With this factor in their favour, it amounts almost to a certainty that their vessel, if dismasted in a storm, would be carried eventually to the immediate neighbourhood of the Marquesas Islands.

The only instance, however, on record, of a long westward voyage having been attempted is that made by the Incan prince, Tupac Yupanqui, in the reign of his father Pachacutec (1421–78). According to the account written by Sarmiento de Gamboa (Hakluyt Society, 1907), shortly after the Inca had conquered the coast and islands of the Gulf of Guayaquil, some traders were brought to him, who stated that they had come by sea from the west in sailing vessels. Their marvellous stories of the riches of their island home fired his imagination; he resolved to visit these wonderful islands and gain renown by their conquest. The construction of a mighty fleet of balsas was ordered; in the preparation of these vessels for a voyage of uncertain duration, we may rest assured that Tupac Yupanqui would take precautions to ensure that the balsa logs of which they were constructed should be specially treated to obviate loss of buoyancy due to absorption of water. As no timber is available in Peru and Ecuador so light and buoyant as that of the balsa tree, we may safely infer that care would be taken to protect the logs from this known danger of absorbing water; what means were taken to effect this protection we do not know except that the obvious remedy would be to coat them with some waterproofing solution or substance—it may have been wax, grease, resin, pitch, or some composition perhaps of lime, resin and oil such as Indian and Arab sailors use for the paying of the bottoms of their boats. (See note on p. 61.)

When the balsa fleet was ready, the Incan prince embarked thereon a host of soldiers and set sail for the west. After the lapse of nine months, or, as some told the Spaniards, 'about a year', he returned victorious with the spoils of the islands—a number of prisoners, dark-skinned people, much gold, a throne of *latón* (literally brass, but more probably some other alloy of copper), and the skin and jawbones of a horse (?). Some authorities, including Sir Clements Markham, consider that the islands visited were the Galapagos, discovered by Sarmiento de Gamboa in 1567; as it is Gamboa who tells the story of the Inca's expedition, it is natural that he should wish to identify *his* islands with those visited by the Inca; if these islands were indeed reached, the skin and bones of the reputed 'horse' may have belonged to a sea-lion, such as the huge male which I once found basking on a sandy beach on Charles Island in 1924.

As for the possibility that any Polynesian islands were found, this is immediately disproved by the mention of gold and *latón*; neither is found either in the Galapagos or in Polynesia. But both gold and copper are met with in Panama, and all the people of Central America were familiar with both metals.

To have found 'black people' (Melanesians?) living on an island where gold deposits occur, the Inca would have had to reach the Fiji Islands; this would have entailed a double voyage so immensely long and difficult as to be quite beyond the capacity of the Peruvian sailors of that period, who seem to have had neither love of exploration nor any of the sea-lore and knowledge of navigation so marked a characteristic of the Polynesians and Micronesians.

That the Galapagos Group was not the only place visited by Tupac Yupanqui seems to be confirmed by the fact that they were uninhabited when found later by Gamboa, and because neither gold nor any remains indicating former human occupation have ever been found there. A location possessing all the attributes necessary to fit in with the story of the spoils brought back by the Inca's expedition cannot be indicated with any certainty; the islands and mainland of the Gulf of Panama seem to be the locality most likely to have been raided by the Incan armada, but I am strongly inclined to think that the Galapagos Islands were visited on the way there.

Lothrop's view that the expedition could not have reached the group because of the difficulty of finding its way thither without charts and navigational instruments may be discounted; we may be sure that the Inca's captains would distribute the fleet in such manner that the balsas would sail in line abreast, separated from each other by a considerable distance while still keeping in sight of one another; this formation was the one best suited to achieve success when searching for the group of islands lying to the westward concerning which vague rumours were then current in the Peruvian ports.

These rumours must have originated from stories of an archipelago of considerable size seen far to the westward by the crew of some balsa blown seawards, far off its coastwise course.

If the Inca's expedition was inspired by these rumours, it is obvious that the voyage would begin by following a westward course. When and if the Galapagos were reached, their lack of inhabitants must have proved a grievous disappointment—no loot of any intrinsic value was to be obtained. Under these circumstances the commander would seek counsel with his sea-captains. Those of them who had coasted northward to Panama would tell of the wealth of gold ornaments possessed by the chiefs of that country, and this would suggest that a raid on some of the important towns would yield booty rich enough to compensate for the failure to find the Galapagos worth attention.

If this proposal were adopted, a northerly course would take the fleet to the mainland of Panama. Gold was very plentiful in that land at the period in question, and golden ornaments would certainly have formed part of any booty brought back when raiding parties went ashore. If some of the people captured were of darker skin than was then usual among Peruvians, this would be sufficient to give rise to the story that dark-skinned prisoners formed part of the plunder obtained.

Having visited the Galapagos and much of the coastline of Panama and Colombia, I am satisfied that this suggested sequence of events furnishes the most feasible and probable explanation of the course taken by the Inca's fleet on this memorable expedition.

The call made at the Galapagos would give a welcome opportunity to refit and to obtain fresh supplies of dried meat and fish. We may be sure that some of the giant tortoises peculiar to these islands were taken aboard to form a reserve store of livestock for use should the voyage be unduly prolonged, in the same way as was the common custom of whalers in the early decades of the nineteenth century. The fish, so plentiful in the waters around the islands, would supply a further addition to the larder, and if some of the Incan soldiers killed a sea-lion on the beach, they probably carried off its skin and jawbone as trophies, and jerked some of the flesh.

During the years immediately after the coming of the Spaniards, the tale seems to have become embroidered wellnigh out of recognition. For example, mention of the skin and jawbone of a horse suggests the insertion of a topical allusion to the wonderful creature ridden by the Spanish invaders; it is easy to understand how the skin and bones of a sea-lion might be 'converted' into those of a horse when the story was retailed to the Spaniards.[1]

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[1] It is worthy of note that formerly the walrus was commonly termed 'sea-horse' by British sailors. It appears under this name in Captain Cook's account of his exploration of Bering Strait in 1778. This name is certainly more suitable for application to the sea-lion, which has the same build and general appearance while lacking the unequine tusks of the walrus.

Lothrop (1932, p. 238), besides denying the ability of the Inca's expedition to reach the Galapagos, is also unable to believe that the voyage was continued to Polynesia. A fatal objection to any such prolonged voyage, he says, or rather meant to say, is the inherent inability of a log balsa to keep the sea 'long enough to complete such a voyage'[1] owing to the absorbent quality of balsa wood, which soon loses its buoyancy unless frequently taken ashore and dried. Certainly no ordinary, untreated balsa raft could make a prolonged oversea voyage unless the Inca's seamen knew of an effective method of treating its absorbent logs with some kind of waterproofing composition as already suggested. This is likely to have been a preparation of gum, resin or wax in some solvent, rubbed over the exterior of the logs in the same way as the Cayapa Indians of the interior of Ecuador coat the exterior of their dug-out canoes with beeswax to protect them from the danger of losing buoyancy (Lothrop, 1932, p. 230). If, as we have been told, the Ecuadorian sailing balsas once plied south to Paita in Peru, and northward to Colombian ports, it seems reasonable to conclude that some waterproofing application was employed to enable these fairly lengthy voyages to be performed and the return trip to be made without the necessity and labour of beaching and dismantling the whole structure for the purpose of drying out the component logs. The South American Indian of Incan times was certainly not less ingenious than the ancient Irish, who carried a supply of butter with them on long coracle voyages for the purpose of smearing it over the hide covering of their frail craft to prevent decay and of daubing it over the seams to keep them watertight (Hornell, 1938, sec. 3, p. 79); their descendants to-day coat the canvas, which is their substitute for hide, with tar and pitch. In ancient Peru and Ecuador, forest products alone were available, unless traders brought pitch from Trinidad or Venezuela; beeswax and vegetable gums, and perhaps some crude form of tar, would be the local alternatives. (See note on p. 61.)

Omitting as improbable the possibility that Incan sailors ever voyaged westwards with the specific object of finding land except on the one historic occasion already mentioned, there remains the question of whether unpremeditated or involuntary voyages may have been made towards the Polynesian Islands by some of their great sailing balsas when dismasted and rendered unmanageable by an easterly or south-easterly gale. If carried towards the west or north-west by the storm, the forlorn craft would come under the influence of the South Equatorial Drift; thenceforward it would progress gradually towards the Marquesas Islands; if it missed going ashore there, the craft would drift on through the Paumotus to the Society Islands, provided that the Paumotus were passed without final disaster.

That this presumed sequence of happenings is to be accepted as fact and not unsupported fancy is proved by the story of the drift voyages of two modern derelicts authenticated by the owners of the first, Messrs Gracie, Beazley and Co. of Liverpool, and by the Secretaries of Lloyd's Corporation and Lloyd's Register of Shipping, in regard to the second. To the owners named I am indebted for their great courtesy in looking up old records containing essential information; I also tender thanks to the officials of the two Lloyd's institutions for the help readily accorded; nor must I omit to thank Monsieur Le Brunnec, the Breton storekeeper of Atuona in the island of Hiva-oa, for drawing my attention to these involuntary voyages, one of them an epic of the sea so fantastic, so full of human interest, of despair, hope and courage, that it is with reluctance that I condense it and omit details of the high-lights and tragic shadows.

The more notable of these instances is the dramatic account of the capsizing, and eventual stranding after a lengthy voyage as a derelict, of the full-rigged ship *Dagonar* of Liverpool, a steel vessel of 2665 tons gross, built in 1892, at Southampton.

Sailing out of Callao Bay on 23 September 1913, bound in ballast for Taltal, a port in Chile, the *Dagonar* ran into a violent gale from the south-east on 7 October; two days later a terrific squall struck the ship, throwing the ballast into the port wing; the next lurch threw her on to her beam ends. A luckless attempt was made to launch a boat—it was smashed against the ship's side and three men were lost. The captain was killed shortly afterwards.

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[1] Owing to a printer's error, this author has been made to state the opposite, that the balsa (*jangada*) has 'inherent ability to remain at sea long enough to complete such a voyage'.

The position when the ship capsized was subsequently reckoned by the First Officer to be approximately: latitude 31° 45′ S., longitude 85° 27′ W.

With great difficulty the masts were cut away, but little relief was obtained. In this perilous condition hope was revived in the early hours of 10 October by the sight of a green light approaching. The last rockets were instantly sent up and an answering signal received. At daybreak the vessel which had so providentially arrived on the scene proved to be the French four-masted barque *Loire*, of Dunkirk.

The miracle had happened, but for three dreadful days of misery and anxiety, during which the weather was too stormy to attempt a rescue, the *Loire* tacked to and fro, sometimes rounding the stern of the *Dagonar* to cheer her crew with the assurance that the Frenchman had no intention of abandoning them until rescue became possible. This was accomplished on 13 October when a gallant attempt successfully took off the survivors during a lull in the weather. The position was then latitude 28° 58′ S., longitude 87° 4′ W.

From the time when the *Dagonar* capsized (9 October) until the rescue on 13 October, the helpless vessel was drifted by the Peru Current about 180 sea miles in a direction generally N. 30° W. This, normally, should have brought the derelict within the influence of the south-eastern section of the South Equatorial Drift. Thereafter, it might be presumed that her course would veer more and more towards the westward until it became due west. On 28 October, a passing vessel sighted the drifting hulk in latitude 27° S., longitude 95° W. (letter from the Secretary, Lloyd's Register, dated 5 October 1944). Continuation of this westward course would take the *Dagonar* into the vicinity of the Marquesas Islands; judging from the normal run of surface drift in this part of the South Pacific Ocean, we should expect that she would then drift slowly south-west, towards the northern Paumotus. If she passed safely through the thickly scattered islands of this 'Dangerous Archipelago', the average course of drift would then take her into the neighbourhood of the Society Islands, where we know that the ship stranded eventually on the coastal reef of the small island of Mopeha, near Raiatea. The date when she went ashore is given vaguely as 'early in 1914'.

That the course above outlined is the one to be expected is proved by the result of drift-bottle experiments initiated by the U.S. Navy Department. By the courtesy of the Hydrographer of H.M. Navy, I have been given an opportunity to study the recorded drifts of certain seven bottles liberated during the present century at various positions well out to the west, off the Peruvian coast, ranging between longitude 92° 10′ and 112° 30′ W., and latitude 0° to 20° S.[1]

Without exception these bottles began their voyages by drifting south-westwards towards the northern islands of the Paumotus, either passing through this archipelago or between these islands and the Marquesas Group. One went ashore in the Paumotus, four reached Fiji, another stranded on an island (Futuna) to the north of Fiji, whilst the seventh, after passing in safety through these island dangers, stranded in Torres Strait, upon the south coast of New Guinea, after a remarkable voyage of some 7225 sea miles.

The importance of these records is that they demonstrate the probability that if a vessel becomes dismasted and out of control off the coast of Peru anywhere between the parallels of 0° and 20° S. and the meridians of 92° and 112° W., she will drift south-west towards the Paumotus and the Marquesas Islands and thence onwards to the Society Islands or to Melanesian islands farther west.

But it seems that the *Dagonar* did not follow this route, though the eventual stranding was on an island in the locality where she might have stranded had she taken the normal course above outlined. According to information received since this note was begun, the derelict was sighted by passing vessels on two other occasions besides the one already mentioned. Both were in positions far to the south of what we would have expected. They were:

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[1] Given on the reverse of *U.S. Pilot Chart*, no. 2601, for December 1924 and January/February 1925.

(*a*) on 4 February 1914 in latitude 26° 33′ S., longitude 122° 41′ W. by the American schooner *Inca*,[1] and

(*b*) on 2 March 1914, in latitude 26° 58′ S., longitude 130° 39′ W. by the ship *Asgerd*.[2]

Accepting these records as correct, it would appear that the wreck, after abandonment, was carried to Mopeha along a southern course which passed to the south of Pitcairn Island. The length of this route is about the same as that of a drift along a northern course which would pass to the south of the Marquesas—about 5000 or 5500 miles, performed in about 170 days without allowing much for zigzagging and assuming arbitrarily that the ship stranded on or about 30 March 1914.

The southern drift actually followed in the case of the *Dagonar* shows that in the part of the South Pacific Ocean where she capsized there sometimes prevail conditions of wind and current which may carry a vessel, when out of control, along either of two routes, a northern and a southern, each leading to the same group of islands. The northern route is likely to be followed whenever the wind is favourable or so light as not to affect adversely the run of the normal surface drift leading to fusion with the South Equatorial Current, whereas the southern route is probably of exceptional occurrence. Even so, the fact that on one recorded occasion such a drift course did take place, is presumptive evidence that it has happened on previous occasions.

The northern course appears to be the normal one when vessels become out of control in positions to the north of the 20th parallel of south latitude, and sometimes even a few degrees farther south; to the southward of this region there is great uncertainty as to what direction the drift course of such a vessel may take, provided her position is sufficiently far to the westward as not to be influenced by the northward-running Peru Current. This latter conclusion receives confirmation from study of the *U.S. Pilot Charts* for the South Pacific Ocean. From these it is seen that between the 20th and 40th parallels (sometimes restricted to positions between the 30th and 40th parallels), winds are variable and unsteady, conditions which impart uncertainty to the drift of any vessel out of control within the limits of latitude named.

Off the South American coast, from the equator to the neighbourhood of 20° to 30° S., the south-east trade wind favours a drift that will end in a merging with the westward-running South Equatorial Current.

The second vessel with which we are concerned, the Chilean wooden ship *Hindostan*, of 1629 tons gross, owned by Sñr M. B. Peede, of Valparaiso, was burned out and lost on 8 March 1900, in latitude 123° W., longitude 8° S., while on a voyage from Port Blakeley to Caldera in Chile, loaded with a cargo of lumber. The crew were forced to take to their boats and 'after a voyage lasting eleven days, the current carried them to the Marquesas Islands' (letter from the Secretary, Lloyd's Committee, 12 October 1944). This gives a rate of drift very much greater than the *Dagonar* experienced; the reason for this probably was that progress would be accelerated by the use of sail in the boats, as the officers would be anxious to reach the islands as quickly as possible.

The story of a third voyage, ending in a drift which cast the vessel ashore eventually not far from where the *Dagonar* stranded, is less well documented. I heard of it first when in the Marquesas in 1925; it concerns an American barquentine said to have been named the *Red River*, laden with a cargo of lumber, on her way to Callao. She is reputed to have sprung a leak off the South American coast; the captain decided to go before the wind, blowing strongly from the south-east. On reaching the vicinity of the Marquesas Islands the crew abandoned the vessel, which drifted to the south-west and was eventually found derelict off Raiatea in or about 1919.

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[1] According to B. Lubbock in *The Last of the Windjammers*.

[2] Information received from Lloyd's Corporation (1 May 1945).

Unfortunately I have, as yet, been unable to obtain confirmation of these particulars. In view of the accuracy of the information given by the same informant regarding the course of events in the case of the two other instances here detailed, I feel inclined to believe that the facts are substantially correct, though it may be that there has been some mistake in regard to the name of this third ship.

Omitting consideration of the third instance of drift voyages because of the need for fuller information, we are able now to see how the other two demonstrate how possible it was during the centuries of Inca domination in the north-west of South America, for the Peruvian sea-going balsas, if coated with some form of waterproofing, to be drifted, when dismasted in a storm, to one or other of the eastern Polynesian islands and with the crew alive, if there were aboard a good supply of fresh water and a sufficiency of food. The ordinary provisions carried would comprise usually a quantity of edible roots and tubers, such as those of the sweet potato; there would often be a supply of various fruits containing seeds from which new plants could be raised. Sometimes part or even the whole of the cargo might have been made up of such vegetable products.

So long as food and water lasted, a prolonged voyage aboard a balsa, even if crippled by a gale, would be easily bearable by the stoic Indians of Peru; if they eventually struck an island in the Marquesas or in the Paumotus, and if they escaped death at the hands of the natives, we may be sure that they would indicate the food value of the tubers and roots and fruits that remained uneaten. If the sweet potato were among these, this would receive special commendation, and its Quichuan name would pass into the islanders' vocabulary. This probability would be greatly increased if any women were taken aboard when sailing from Peru. As already noted (p. 46) it is likely that women would be spared, even if all the men were killed.

There can be no proof that introduction did occur in this way, but such a hypothesis is easier to envisage than that of a voyage from Polynesia to the Peruvian coast, with a friendly reception there and a safe return home. As already explained, it is scarcely conceivable that return by the same route could be effected safely. By any other route, return would be equally or even more difficult and dangerous unless they obtained much more information about sea routes from the Peruvians than their knowledge of navigation would be able to furnish.

THE DISTRIBUTION OF THE SWEET POTATO AS ASCERTAINED BETWEEN 1722 AND 1825

Before summarizing the body of evidence presented in the foregoing pages we must know what was the distribution of the sweet potato in the various groups of islands which make up Polynesia when this area was visited by explorers in the eighteenth century and in the early part of the nineteenth century, the period when Europeans and North Americans were most actively engaged in exploring and charting the islands of Oceania. We have to know, in particular, what were the chief centres of the cultivation of this tuber and what was its distribution in the outlying or peripheral islands. These latter comprised the trio, Easter Island in the extreme east, Hawaii in the extreme north, and New Zealand in the distant south-west.

The available evidence for the answering of these questions is the following:

EASTER ISLAND. Roggeveen, who discovered the island in 1722, and all subsequent visitors down to Beechey in 1825, speak of the sweet potato as abundant there; it was grown in large plantations and was recognized as one of the most important of the islanders' food supplies.

HAWAII. Cook, who discovered the group in 1778 and those who followed in his track during the next quarter of a century, testify to the abundance and excellence of the sweet potatoes grown there.

NEW ZEALAND. Cook and Banks in 1769 and many others agree in their testimony that the sweet potato occupied an important place in the dietary of the Maoris of North Island,

and later it was found in common use on the northern section of the east coast of South Island.

Conversely, the evidence of eighteenth-century voyagers through Central Polynesia tends to belittle the importance attached to the sweet potato in the dietary of the people of this region. Dixon (1932, pp. 45–9) goes into details which may be summarized as follows:

In the PAUMOTUS (Tuamotus), an archipelago consisting of low coral islands, the physical conditions are unfavourable for the cultivation of the sweet potato, and no old-time references to it are on record. In MANGAREVA (Gambier Islands), Beechey records the sweet potato as of comparatively little importance, but later records point to a revival of its cultivation after the arrival of the early French missionaries.

In the SOCIETY ISLANDS the sweet potato occupied only a minor position in the islands' food production. In the COOK ISLANDS, Williams (1837, p. 578) specifically attributes its introduction to missionary enterprise. In TONGA it also had little importance as indicated by the fact that Mariner does not mention it save in his vocabulary; in SAMOA it is again a late missionary introduction and was not in general use according to Turner (1861, p. 192), who is explicit that its introduction was due to European intervention.

The outstanding conclusion to be drawn from these facts is that the cultivation of the sweet potato was of minor importance in Central Polynesia prior to the arrival of European missionaries in the early part of the eighteenth century, whereas it was flourishing in the three islands or island groups situated at the points of the Polynesian triangle—Hawaii, Easter Island and New Zealand—when these were visited by Europeans in the eighteenth century and in the first quarter of the nineteenth.

To be in profuse cultivation in peripheral islands so distant from one another, presupposes a distribution at an earlier period throughout the whole area; the small importance which it had in the central area at the time of eighteenth-century exploration appears to have arisen from one or other of two factors or from a combination of the two; either some factor or factors were present there which adversely affected its cultivation, such as a high, humid temperature, or else there were other food supplies available in abundance, better adapted to suit the seasonal conditions of temperature, rainfall and sunshine prevailing there. For example, the Polynesian breadfruit (*Artocarpus communis* Forst.) has superior importance in the central area where the islands have a warm, damp climate; there this handsome tree usually bears four crops in the year, with the further virtue that its fruit's flesh, when baked and pounded, may be stored in a fermented condition for a prolonged period, to be eventually baked as required.

In Samoa the swollen root of taro (*Colocasia antiquorum*) competes with the breadfruit as the people's staple diet, while in the Marquesas Islands, although breadfruit and taro furnish the principal vegetable foods of the islanders, in those seasons when the breadfruit fails and famine afflicts the land the people turn to the sweet potato for relief. This they do because of the ease with which the tuber is propagated and the rapidity of its growth, for it matures within four or five months. Taro, on the contrary, takes twelve months to become fit for lifting (Malo, 1903, p. 67).

Unlike the breadfruit which flourishes in moist heat, the sweet potato is suitable for cultivation on dry upland plains and slopes (Malo, 1903).

SUMMARY OF CONCLUSIONS

1. Of the principal food products obtained from plants which were in general use in Polynesia and somewhat doubtfully in parts of Melanesia as well, when these islands were first visited by Europeans, the only one which seems, without reasonable doubt, to be a native of America is the sweet potato (*Ipomoea Batatas*). Nearly all others of importance, such as taro, yams and the coconut, are derived, on the contrary, directly from species native to India, south-east Asia or Indonesia; these appear to have accompanied those migrating bands which pushed eastwards into the Pacific at some remote period, to

become specialized into the Polynesian race; a few, such as the Polynesian breadfruit (*Artocarpus communis*), though ultimately derived from the same area, have evolved locally into new species and varieties, characteristic of their Oceanic habitat.

2. The problem before us resolves itself mainly into consideration of how and when the one plant exception, an American-born species, was introduced into the island world of Polynesia.

3. Failing the possibility of diffusion along a land bridge, we are obliged to assume human agency as the means of distribution for the quite adequate reason that this product carried with it the name by which it is known in the Quichuan language of South America. Once introduced, the plant, together with its Quichuan name in some modified form, became widely distributed throughout the Polynesian Islands by local seafaring activity. This diffusion must have taken place at a very early period, seeing that the cultivation of the sweet potato had time to spread from the focal point of first introduction to every group throughout Polynesia, however distant, as well as to overflow into many islands in Melanesia by the time when Europeans were making their major discoveries in the Pacific in the eighteenth century. This diffusion may have taken centuries to complete, seeing how widely scattered the island groups lie and that intercommunication between the centre and the peripheral islands ceased after the close of the heroic age of Polynesian voyaging which ended sometime about the fourteenth century. After that we have no records of voyages from Tahiti to New Zealand, or to Easter Island, and none to or from Hawaii and Tahiti, whereas it is known that the sweet potato was held in high esteem as a valuable foodstuff by the peoples of Hawaii, New Zealand and Easter Island at the time when these islands were first visited by Europeans.

4. Consideration of the foregoing proves that the cultivation of the sweet potato in Polynesia dates back to a period sufficiently early to enable the question of pre-Columbian contact between Oceania and America to be answered in the affirmative, with the proviso that this intercourse was exceptional, strictly limited, and probably occurred with effective result on one occasion only.

5. How this pre-Columbian contact and the resulting introduction of this tuber into Oceania were effected, we cannot definitely decide on the data available. Two alternative explanations have been envisaged: either Polynesian mariners sailed to Peru, learned there the Quichuan name, and thence returned with a quantity of sweet potato tubers in a condition suitable for planting; or Quichuan-speaking people, in vessels of the sea-going balsa type, were drifted to Polynesia where the crews were enabled to plant some tubers in the islands which they reached. I incline to consider the latter explanation to be the more probable: the Polynesian names for the sweet potato are undoubtedly variations of the Quichuan term *kumar* or *kumal*.

6. *Did Polynesians voyage to South America and return?* That a Polynesian voyage of discovery may have reached South America between the tenth and the fourteenth century is certainly possible when we consider the extremely long voyages successfully accomplished by Polynesians during this period of intense maritime activity. It may, however, be argued fairly that had such a voyage been made, its memory would have lived in tradition, as have the voyages between Central Polynesia and New Zealand, Hawaii and Easter Island.

The only route to South America that could conceivably have resulted in success is that from Tahiti or Samoa, via Mangareva, Rapa and Easter Island. After resting at Easter Island, the voyagers would soon have fallen in with the northbound Peru Current; this would prove of great help and would lead to a successful landfall in Peru, if an easterly course were continued, gradually edging across the current.

A voyage from the Marquesas Islands would have been much more difficult and uncertain, and this route may be eliminated at once because the drift of the South Equatorial and Peru Currents would be contrary over the entire distance to be traversed; the length of the voyage would also be considerably greater than that by Easter Island. The winds also would usually be adverse.

7. If the voyage were made via Easter Island, the factors of winds and currents, so extremely favourable on the outward journey, would operate equally adversely for a return in the reverse direction; any chance of succeeding would be so reduced that it becomes negligible and has to be ruled out as hopeless.

Only by steering a course north-west from Peru would it be possible for the return to be made; this would lead via the Marquesas Islands to the Society Islands. This fact could not be known to the Polynesian voyagers; although unlikely, it is possible that information pointing to the favourable run of the currents on the first stage of this route was available from some of the Peruvian balsa sailors; if so, a return voyage by this route may have been effected. Every fact considered, it seems extremely doubtful if any Polynesians ever succeeded in making the return voyage.

8. *Peruvian drift voyages to Polynesia.* The prominence given in Peruvian history to the expedition of the Incan prince, Tupac Yupanqui, is evidence that a long voyage westwards was a most exceptional event. Nowhere have we any suggestion, apart from this solitary exception, that the ancient Peruvians had either inclination or necessity to go voyaging in search of new lands.

But there remains the possibility and even the probability that transmission of the sweet potato may have resulted from an involuntary drift voyage from Peru, consequent upon the dismasting and crippling of a balsa raft when on a coastwise voyage. When such an occurrence happened, the northbound Peru Current would take charge until a position was reached where the northward current merges into the South Equatorial Drift. This in turn would take charge and would carry the helpless craft westward to the Marquesas Islands, where, granted a friendly reception, any tubers uneaten would be taken ashore and planted, the Quichuan name going with them. This hypothesis is rejected by Lothrop owing to the known inability of balsa logs to remain buoyant for more than a limited period; this, he contends, is a fatal objection to the idea that balsa sailing rafts could keep the sea long enough to permit of lengthy voyages being contemplated or made inadvertently. But this defect may be remedied. In Ancient Egypt and in Assyria reed-bundle craft were made water-resistant when this was necessary by a coating of bitumen, just as the 'bulrush ark' of baby Moses was waterproofed. In ancient Peru a similar result may have been obtained by coating the logs with some preparation of beeswax in the way that certain Indians of Ecuador waterproof their dugouts; gum or resin are alternatives. Balsa wood so treated would be well adapted to remain buoyant long enough to enable a drifting balsa raft to reach the neighbourhood of the Marquesas Islands.

9. Proof of the value of the Peru Current and South Equatorial Drift for the fortuitous transport of objects of material culture from South America to Polynesia is afforded by certain drift-bottle experiments of the U.S. Hydrographic Department, which indicate that bottles thrown overboard off the coast of Peru drift into the South Equatorial Current drift and are carried by it past the Marquesas Islands and through the Paumotus to strand upon the islands of Central Polynesia and of eastern Melanesia. The drifts of derelicts in this region add weight to this evidence.

10. As an alternative to the pre-Columbian introduction of the sweet potato, whether by Polynesians or by South American Indians, Friederici has championed the view that this plant was introduced into the Marquesas Islands and into certain Melanesian groups by the Spaniards under Mendaña and Quiros in 1568, 1595 or 1606, the years when they had opportunity to plant the tubers on the islands which they had discovered.

This plausible explanation, which, if well founded, would solve the problem in an easy and satisfactory manner, cannot be accepted for the following reasons: (1) there is some evidence that the sweet potato was already under cultivation in Oceania at the period indicated; (2) there is no adequate proof that the Spaniards did introduce the cultivation of this plant at any of the islands visited even so early as 1568; the reasoning that this did occur is based entirely upon 'probabilities', particularly upon the common custom of Spanish explorers to plant seeds and roots of useful fruits and vegetables at any place which they had hopes of colonizing or occupying; and (3) had the sweet potato been introduced even so early as 1568, this would not have allowed sufficient time for its diffusion to Easter Island, New Zealand and Hawaii by 1722, 1769 and 1778, the years when these islands were discovered respectively by European explorers, because long inter-island voyages, such as those from Hawaii to Tahiti and those from Tahiti to Easter Island, *had been discontinued after the close of the fourteenth century.*

What appears reasonably certain is:

(*a*) That there was at least one instance of effective contact between Polynesia and South America in the pre-Columbian period.

(*b*) That the sweet potato's introduction into Polynesia was due to this contact arising from an isolated incident.

(*c*) Whether this introduction was due to Polynesian voyagers who sailed to America and took back the sweet potato on their return, or whether its diffusion originated in an involuntary drift voyage from Peru, must remain uncertain; I incline to favour the second explanation as being much the more likely.

11. Whether the sweet potato was already present in the Marianas at the time of Magellan's discovery of the southern islands of this group is problematical. What is certain is that its cultivation was encouraged in Guam from the sixteenth to the nineteenth century by the Spanish authorities, in order that supplies might be available to passing ships on voyages between Acapulco and Manila in particular. As a consequence its Mexican name of *camote*, a corruption of the Nahua word *camotl*, was adopted into the languages spoken in the Marianas and the Philippines.

In conclusion, I wish to express my deep obligation to Mr I. H. Burkill for his readiness to afford me much valuable advice out of his wide knowledge of this subject. The help which he has afforded me has been of the greatest service in the preparation of this paper, and for this I am most grateful. I am also under obligation to the Hydrographer of H.M. Navy and to the Hydrographer of the United States Navy for much courteous assistance.

Postscript. Regarding the waterproofing of canoes referred to on pp. 52 and 54, Mr Burkill has drawn my attention to the statement by Herrera that the dugout canoes of the natives of the Lesser Antilles had their 'sides raised by canes, daubed over with bitumen' (Quoted by H. W. Krieger in his article on 'The Aborigines of... Hispaniola', in *Ann. Rep. Smithson. Inst.* 1929, p. 482).

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Note. For bibliographies of wider range see Dixon (1932), Lothrop (1932) and Hornell (1936).

An 'Indigenous Induced' Phormium tenax Forst. swamp in New Zealand.

By A. L. POOLE, New Zealand Department of Scientific and Industrial Research.

(With Plates 1 and 2 and 2 Text-figures)

[Read 10 May 1945]

Two species of the liliaceous genus *Phormium* are found in New Zealand, *P. Colensoi* Hook. f. and *P. tenax* Forst. Both species are giant iris-like plants with short stocky rhizomes bearing long, keeled, broad-bladed, coriaceous leaves. *P. Colensoi* is the smaller with a somewhat lax drooping habit, reaching a height of 3–4 ft. Its typical habitat is wet mountain sites, but it also occurs extensively on steep cliffs along the coast. *P. tenax* is a stronger, stiffer and taller species, reaching a height of 7–8 ft. It is typically a lowland species confined to swampy habitats, but sometimes it grows on dry land.

The leaf fibres (bundles of fibre cells) of *P. tenax*—classed in the category of hard fibres of which sisal (*Agave sisalana*) and Manilla (*Musa textilis*) are representative—were used by the Maori prior to the advent of the white man in New Zealand. The Maori selected good-fibred strains and grew them around his dwellings. The white man, on his arrival, soon found the fibre of economic importance, and accessible areas of *Phormium tenax* were worked. At first this was done by Maoris using their own method of stripping by shells, but before long stripping machines were introduced and a thriving industry developed.

The areas worked were in the main swamp areas found in the lower reaches of large rivers where they overflowed their banks extensively. To make them more manageable, these areas were partially drained as they were worked. This operation had the effect of extending the phormium stands to form an 'indigenous induced' community, in appearance as natural as the original.

Such apparently natural stands were called by Dr Leonard Cockayne 'indigenous induced phormium associations'. He describes them as follows:

'In various parts of New Zealand proper, especially where large rivers overflow their banks, there are extensive areas of ground, perhaps extremely wet in winter, but quite dry in summer, occupied by bushes (tussocks) growing closely of *Phormium tenax*, making apparently a pure association. To one unversed in this class of vegetation, it would unhesitatingly be considered primitive, yet it has arisen solely through draining the *Typha*-phormium Swamp described in part II. Nor would it remain stable for long were it not that various invading species are removed by the owners of the "flax-swamps" so called.

'As has been explained, the primitive swamp is wet at all seasons and contains abundance of *Typha angustifolia* (in a wide sense), but, as with *Phormium*, it only occurs—more or less stunted—here and there in the shallowest water or fringing the margin of the swamp. Into the latter deep drains are cut, its water-content is greatly lessened, and in a year or two the phormium present attains its full dimensions: then the substratum becoming drier the *Typha* will languish and young phormium plants come up thickly all over the drained ground. In a few years such attain their full dimensions and the former swamp will be almost pure Phormium 3·5 m. high, under favourable conditions.'

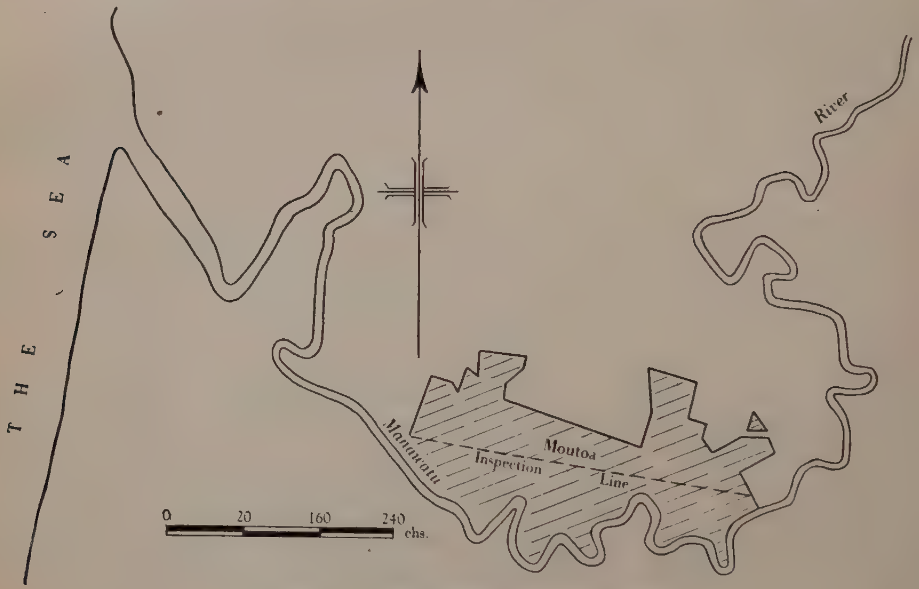
At one time these indigenous induced areas were extensive in the lower reaches of some of the larger New Zealand rivers and provided fibre for a lucrative overseas trade. The peak of their extent and exploitation coincided with the 1914–18 World War. Intensive working during and immediately following this war led to excessive drainage. This in turn created habitat conditions unsuitable to the species and the phormium community quickly disappeared. Competition in overseas markets from sisal fibre hastened the trend. The land was finally cleared and turned to dairy-farming. Some phormium stands remained in the lowest lying areas which were subject to severe flooding.

Recently one of the largest remaining areas near the mouth of the Manawatu River, which flows to the west coast of the North Island, was acquired by the Government. This is to be developed as a phormium estate in an endeavour to assist the re-establishment of the industry. The first step, to serve as a basis in the development of the estate, was the carrying out of an ecological survey, upon which the writer was engaged. This survey revealed that the history of the vegetation of the estate was similar to Cockayne's description of indigenous induced phormium areas.

The survey and the results will now be described in some detail.

DESCRIPTION OF THE ESTATE

The area purchased by the Government, known as the Moutoa Estate (Text-fig. 1), is some 4500 acres in extent and lies along the north bank of a meandering section of the Manawatu River, about 10 miles from its mouth. It occupies a very shallow, extensive basin with contours ranging from 4 to 20 ft. above mean sea-level. The highest contours are along the river bank where floods spill over and deposit sand and silt, and again at the limits of the inundations where the ground begins to rise to low hills. The lowest contours are along the middle of the inundated area, parallel with the general flow of the river. With the exception of portions of the river bank, the area is subject to flooding on an average of two or three times a year. These floods may occur in any season.



Text-fig. 1. *The Moutoa* Phormium *estate.*

The high river banks are dry at all times of the year. The original vegetation was cleared early and the ground is now either cropped or grazed. The lower ground is dry in summer but wet in winter and is covered with dense swamp vegetation, the distribution of whose communities is closely related to the height of the water table.

The soils are derived from recent sediments deposited by the Manawatu River with the inclusion of peaty phases in the lowest lying portions. The sedimentary deposits range from sands and sandy silts on the river banks, where the coarser river-borne material has been deposited during floods, to silt and clay loams on the lower ground away from the banks.

All these recent sedimentary deposits are underlain at depths of from 18 in. to 12 ft. by a more consolidated bluish clay loam on which are the timber stumps of an old forest. Where peaty soil phases have shrunk through drainage, these stumps sometimes appear above the surface.

All soil types show less acidity than is usually associated with meadow soils. They can also be regarded as fertile as far as plant food requirements are concerned.

Method of vegetation survey

In carrying out the survey use was made of an inspection line running east to west through the length of the estate (Plate **1**, fig. 1). From this, offset lines at right angles running to the river and to the inside boundary of the estate were made every 10 chains apart. These offsets were then cruised by chainmen and mappers, and the plant communities were mapped over the whole area.

In determining the significant communities a study was first made of a map made from aerial photographs. From this it was possible to pick out vegetation types which were then inspected in detail on the ground.

The distribution of the plant communities so obtained was compared with maps showing contours at narrow intervals and soil types; comparison was also made with the character and distribution of the original vegetation, the necessary data concerning them being obtained from old survey maps, 'remnant' species and communities, and an early knowledge of the estate provided by old settlers in the neighbourhood.

In the following sections the virgin vegetation as depicted from the evidence available, the 'indigenous induced' phormium communities, and other communities caused by man's interference, are described. By piecing together the history of these communities, it is possible to formulate the optimum habitat conditions for high-yielding phormium stands.

Virgin vegetation

Along the higher contours of the river bank *Podocarpus dacrydoides*, semi-swamp forest, existed. Remnants of this forest still exist in a fairly well-preserved state, but the greater part was cleared in the first days of settlement to give place to pasturage and cropping. In the semi-swamp forest it was the dominant tree. Other prominent trees were *Laurelia novae-zelandiae* and *Eugenia maire*. The under-stories contained a number of *Coprosma* spp., hybrids between some of them, and tree ferns (mainly *Dicksonia squarrosa*), and the floor was covered with a great number of ferns, particularly of the genus *Blechnum*. The lianes, bush lawyer (*Rubus australis*), *Muehlenbeckia australis* and *Parsonsia heterophylla* were greatly in evidence.

At the lower levels the ground became wetter and the forest gave way to a belt of swamp scrub in which *Coprosma* spp. would be dominant. Cabbage trees (*Cordyline australis*) would also be present and phormium bushes would begin to appear.

Under still wetter conditions the scrub belt would be replaced by a phormium belt which would be comparatively narrow, as the swamp varieties of this plant grow in a narrow range of water-table conditions only. This belt would in turn pass into extensive areas of *Typha angustifolia*, which plant grows in a wider range of water-table conditions than phormium.

Present-day evidence tends to show that both phormium and typha would grow highly gregariously and have few associated species.

In the lowest parts typha would be replaced by shallow lagoons fringed by sedges (*Carex* spp.), and probably with the sedge *Carex secta* growing scattered throughout. The lagoons would be kept filled by frequent flood waters.

VEGETATION CHANGE SUBSEQUENT TO WHITE SETTLEMENT

As already mentioned, the river bank forest was removed in the first days of settlement. Then about 1875 the estate was sold with the object of clearing and development for farming land. The drainage of the interior wet-belts of phormium, typha and of the lagoons began.

This drainage had what must then have appeared an unusual effect. In the typha belt it created water-table conditions suitable for phormium. Typha languished, and the phormium seedlings which are frequently present in large numbers in the Typha community flourished, producing extensive, highly gregarious stands (Plate **1**, fig. 3). Further drainage extended the phormium to part of the areas occupied by lagoons. Cockayne's true 'indigenous induced' areas of phormium, or 'flax swamps' of the settler, had been produced by altering the water table only. The original phormium belt was invaded by a moisture-loving tree, *Cordyline australis*, and swamp shrubs (Plate **1**, fig. 2).

The ambition of clearing the area for farming was never realized. This proved too difficult a task to perform on semi-swamp vegetation blessed with habitat conditions just to its liking, and on an area subject to severe and frequent flooding.

About the time the draining of the estate began, the phormium industry was becoming well established. Cutting of phormium leaf therefore began in 1887.

From 1900 to 1920 the phormium areas were at their peak. Further drainage filled most of the interior low-lying areas with phormium stands. Invading species were continually removed when the stands were cut for leaf every 3–4 years, and in this way the stands were kept very pure.

From about 1920 the phormium fibre industry began a gradual decline. The Moutoa estate was therefore worked less intensively and weed species crept in. Other causes brought about serious deterioration in the phormium stands, and extensive changes took place in the vegetation.

These changes and their causes were:

(1) The easterly portion of the estate, or that mainly within the higher contours, was over-drained from the point of view of optimum conditions for phormium. This in conjunction with the less intensive working of the estate allowed certain aggressive weeds to appear, and, in places, reach serious proportions. Blackberry (*Rubus fruticosus* s.l. and *R. laciniatus*) has increased until it has become subdominant to phormium over extensive areas. In the most easterly part of the estate, which is the best drained, it is co-dominant with phormium.

Another serious weed is tall fescue (*Festuca arundinacea*). This strong-growing, tufted grass has invaded the phormium stands, including some planted stands, within the higher contours of the river bank. Goat's rue (*Galega officinalis*) usually grows in association with tall fescue.

(2) In the westerly portion of the estate, within the low contour belt, shrinkage of the peaty soils has taken place. These areas are now extremely difficult to drain, being but 3 ft. above mean sea-level, and flood waters lie for long periods. The water table is well above ground-level for most of the winter. In the summer flood waters have lain on freshly cut phormium bushes and killed them, making room for the invasion of other species. By this means typha has once again replaced thriving, induced phormium stands. This replacement by typha is shared extensively by beggars' tick (*Bidens tripartitus*) (Plate **1**, fig. 4). We thus have extensive areas of a community almost exclusively composed of the two species, *Typha angustifolia* and *Bidens tripartitus*, the former indigenous and the latter European. In the lowest lying or wettest areas of all the phormium stands have been replaced by two exotic species, occurring singly or together—reed sweet grass (*Glyceria aquatica*) and reed canary grass (*Phalaris arundinacea*).

(3) The most serious encroachment of all has been by the exotic crack willow (*Salix fragilis*) (Plate **2**, fig. 5). When given the opportunity this species grows throughout the

estate on any soil type or under any water-table conditions. About 1880 the species made its first appearance on the estate in a single planted grove. Since then boughs have been used as occasional light tram-line sleepers, for fencing, etc., and twigs have been broken off and dispersed by floods. Many of these have taken root, so that willow groves and single trees now occupy some 25% of the area.

THE PLANT COMMUNITIES AND THEIR DISPOSITION AT THE TIME OF THE SURVEY

We can now compare the vegetation at the time the survey was made—the product of human interference—with the vegetation as it existed in the virgin state. As a result of the changes which have taken place since white settlement, we have in place of the definite belts of vegetation (Podocarpus forest, scrub, phormium, typha, sedges, and shallow lagoon) a mosaic of the following communities:

(1) Phormium.
(2) Typha.
(3) *Festuca arundinacea.*
(4) *Bidens tripartitus.*
(5) *Glyceria aquatica.*
(6) *Salix fragilis.*
(7) Remnant podocarpus forest.
(8) Perennial ryegrass-white clover pasture.

The distribution of these indicates the water-table conditions, and a knowledge of it is therefore of importance in developing the estate for phormium. A brief account of their structure and distribution will therefore be given.

(1) *Phormium* (Phormium tenax) *community*

Phormium occurs gregariously in stands up to 150 acres in extent in areas where it was originally induced and where the water-table conditions must have since remained fairly constant.

In the optimum phase of these stands, phormium leaf up to 40 tons green weight per acre could be cut every 3½–4 years. Individual plants are usually 3–4 ft. apart and of approximately 8–9 fans and up to 8 ft. high. Lack of light allows only a minimum of vegetation on the ground, usually of the sedge *Carex ternaria*, and of the fern *Blechnum procerum*. A few shrubs of *Coprosma* spp. and scattered cabbage trees (*Cordyline australis*) may be present.

Regression phases from the optimum occur with the opening out of phormium. These become more and more open, gradually passing into other communities. The most open stands of phormium which can be worked commercially yield about 5 tons of green leaf per acre. In these stands the 'bushes' are scattered and large with an outwardly spreading circle of 50–100 or even more fans. As the phormium opens in the regressional phases the incoming vegetation is of two types, depending upon whether conditions are wetter or drier.

On the wet side, typha is the first to appear. The delicate balance between typha and phormium is the best indication of optimum conditions for phormium (Plate **2**, fig. 6). Taking the estate as a whole, typha is the most typical dominant and subdominant species in association with phormium. Under slightly wetter conditions, beggars' tick, frequently in association with typha, appears.

On the dry side, phormium is frequently accompanied by much shrub growth consisting of the climber (*Muhlenbeckia complexa* and *M. australis*), *Coprosma robusta*, *C. propinqua* and hybrids between these two coprosmas. In the higher contours near the river bank cabbage trees (*Cordyline australis*) increase in numbers. On certain areas in the east of the estate where drainage has been carried a little too far, but without affecting greatly the phormium stands, blackberry is present. In places it becomes a formidable obstacle to the cutting of phormium leaf. Near the river bank all phormium stands have tall fescue and goat's rue (*Galega officinalis*) in them. As the stands open out the intervening space is frequently monopolized by these two plants. Bindweed (*Calystegia sepium*) is sometimes present. Phormium stands planted in areas along the bank itself include a great deal of tall fescue.

(2) *The raupo* (Typha angustifolia) *community*

Raupo (the British layman's bullrush) occurs in pure, dense stands of considerable acreage where conditions are somewhat too wet for phormium (Plate **2**, fig. 7). In the regressional phases of the community typha is replaced by phormium on the dry side and by beggars' ticks and sweet reed grass on the wet side.

(3) *The tall fescue* (Festuca arundinacea) *community*

This strong-growing, tufted, exotic grass sometimes forms almost pure areas of limited extent near the river banks and along the free-flowing drains (Plate **2**, fig. 8). It is more frequently associated with goat's rue and, in places, phormium. Over extensive areas within the higher contours it occurs as a subdominant to phormium. Its appearance indicates good drainage and comparatively dry conditions.

(4) *The beggars' tick* (Bidens tripartitus) *community*

This introduced annual occurs almost pure in limited areas in the wetter parts. It is more usually associated with typha and phormium. On the wet side, it gives way to reed sweet grass.

(5) *The reed sweet grass* (Glyceria aquatica) *community*

The reed canary grass is usually associated with the reed sweet grass in this community. It is found in the wettest and lowest lying areas of the estate. A favourite habitat is along low-lying drains. Both species are introduced. They spread vegetatively from the margins, frequently forming distinct circular patches.

(6) *The crack willow* (Salix fragilis) *community*

Crack willow, an introduced species, is practically the only willow on the estate and occurs as single trees or groves up to 20 acres in extent. It occupies some 20 % of the area of the estate and is indiscriminate in its habitat. It suppresses all vegetation beneath it except for herbaceous plants.

(7) *Remnant kahikatea forest* (Podocarpus dacrydoides)

This forest has been described above as it would have existed in its virgin state. Its appearance and structure is much the same now.

(8) *Perennial ryegrass* (Lolium perenne) *and white clover* (Trifolium repens) *pastures*

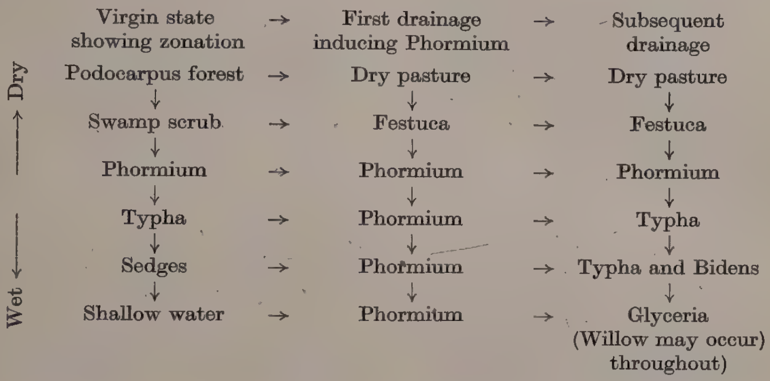
These pastures, dominated by the two species but containing important subdominants also, have been sown along parts of the river bank on areas once occupied by forest. They grow on the driest and best-drained part.

DISCUSSION

Changes in the vegetation from the virgin condition, through the stages brought about by the varying degrees of interference by man, may now be pieced together. The virgin state shows a zonation of plant communities closely correlated with the spatial change in the height of the water table. The limits of their distribution are set by edaphic conditions and competition between the dominants. On the relatively dry river banks where the water table is lowest, *Podocarpus* forest occurs. As the ground-level falls and the land becomes correspondingly more liable to inundation, the water-level is relatively higher and other communities appear. The communities in order are *Podocarpus* forest, swamp scrub, *Phormium*, *Typha*, open water with scattered *Carex* species. In this series *Phormium* occupies a relatively narrow zone.

The first period of change was initiated by draining the wettest areas. This led to the extension of the area suitable to *Phormium* to land hitherto covered by *Typha* and by open water. *Phormium* was also planted on cleared swamp scrub and, to a limited extent, on *Podocarpus* forest areas. The range of soil moisture conditions over which *Phormium* was grown was therefore extended to include land suboptimal for it. By intensive management, however, and the continual removal of competing weeds, both native and exotic, the dominance of *Phormium* was maintained.

The result of drainage in those parts of the area with peaty soil phases was the shrinkage of the peat and a fall in the ground-level until in places further drainage was no longer possible or economic. In keeping with the new conditions of a high water table and excessive wetness, *Phormium* was exterminated and replaced by the native *Typha* and the exotics *Glyceria* or *Phalaris*.



Text-fig. 2. General changes in vegetation consequent upon drainage.

Competition in world markets with other hard-fibre producing plants led to a decline in the phormium industry and to the last and present state in which, with less intensive management, weeds were no longer controlled to the same degree. Some of these now share dominance with the *Phormium* in habitats less suitable to it, but more suitable to the weeds. Thus in areas on the dry side for *Phormium* the exotics blackberry, *Festuca* and *Galega* may become co-dominant with it. But between the relatively dry and the very wet lies a belt in which *Phormium* is still virtually the sole dominant. Thus the *Phormium* (natural, induced and planted) becomes split up into pure phormium and phormium with differentiating co-dominants.

Another exotic, *Salix fragilis*, is less fastidious, for it grows and reproduces freely by vegetative means on all parts of the area: unrestricted it successfully ousts the *Phormium*.

It is a task for the future to discover the conditions optimal for *Phormium*, in particular the relation of the species to the water table, its rise and fall, its duration at various levels, and to find out exactly through what physiological processes (e.g. the supply of oxygen for respiration) the distribution and vigour of the phormium is controlled.

The changes in vegetation resulting from changes in water-table conditions are summarized in Text-fig. 2.

APPENDIX OF MAORI NAMES

kahikatea	*Podocarpus dacrydoides*
karamu	*Coprosma robusta*
maire	*Eugenia maire*
mingi-mingi	*Coprosma propinqua*
pohuehue	*Muhlenbeckia complexa* and *M. australis*
pukatea	*Laurelia novae-zelandiae*
raupo	*Typha angustifolia*

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EXPLANATION OF THE PLATES

PLATE 1

Fig. 1. A survey line passing through *Typha angustifolia.*
Fig. 2. The induced belt of *Cordyline australis.*
Fig. 3. A good area of induced *Phormium tenax.*
Fig. 4. *Phormium* being killed out in a low-lying area. Stems of the invading *Bidens* can be seen between weakened *Phormium* plants.

PLATE 2

Fig. 5. *Salix fragilis* invading *Phormium.*
Fig. 6. *Phormium* and *Typha* in delicate balance.
Fig. 7. *Typha* community.
Fig. 8. *Phormium* and *Festuca arundinacea* near the dry river bank.

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Phormium tenax swamp in New Zealand

Contributions to the Life History and Biology of Digitalis purpurea.
I. The Development of the Ovule. By Comyns J. A. Berkeley.

(With 20 Text-figures)

[Read 26 April 1945]

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I. INTRODUCTION

Some facts relating to the development of the ovule of *Digitalis purpurea* are given by Tulasne (1849), Chatin (1874) and Schmid (1906). The first of these workers was mainly concerned with fertilization and the second with the development of the seed; moreover, both lacked modern technique. Schmid's research is essentially comparative, and on that account is lacking in the detail which it is felt necessary to have for the present purpose. As a consequence an attempt has been made to follow the development of the ovule through its various stages, to check what facts can be deduced from the papers mentioned above, and to produce a more complete picture of the first stage in the life history.

II. SUMMARY OF PREVIOUS WORK

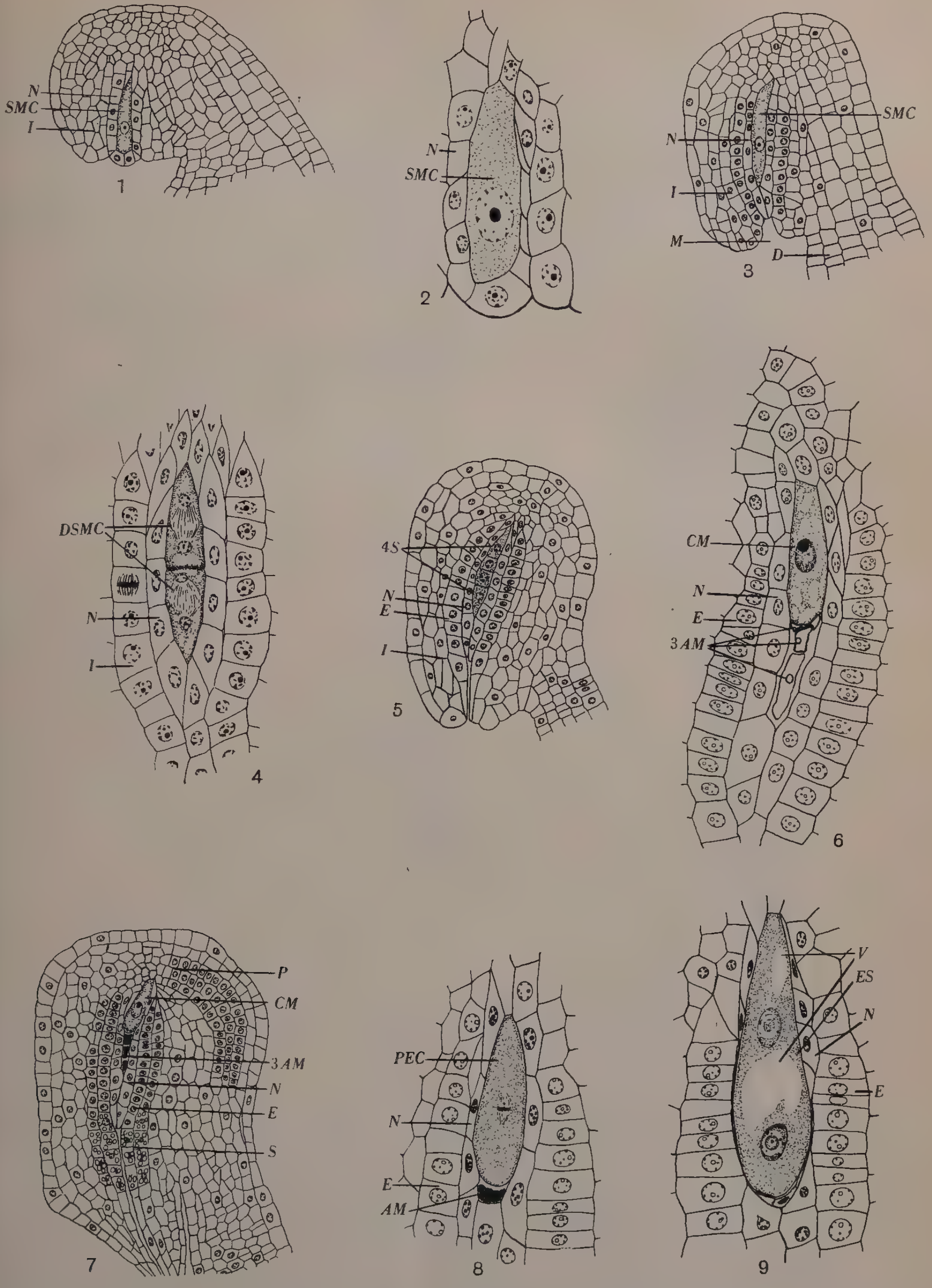
According to Chatin (1874) the ovules are little blunt nipples when the ovary is 1·5–2 mm. long and is surmounted by a conical tubercle in which a somewhat inobvious fork indicates the future stigmas. Just before the integuments appear the ovules are 0·01–0·03 mm. broad. Tulasne (1849) writes of curved ovules in ovaries 2 mm. long. According to him the nucellus develops into a blunt cylinder with a maximum diameter of 0·02 mm., while the integument grows round it so that only 0·02 mm. of the nucellus remains projecting from the weakly curved ovule by the time the ovary has reached the length of 3 mm. Schmid writes that the archesporial cell starts dividing, as soon as the integument has reached the curved surface of the nucellus, to produce in due course four embryo-sac cells of which the hindermost becomes the embryo sac. He states that the development of the embryo sac follows in the normal manner but gives no details either of the development or of the mature structure of the embryo sac except for a small figure of the latter and a statement that it is ventricose in its front third. Tulasne indicates by drawings of the entire ovule, and Chatin states, that the integument continues to grow while the ovule is becoming anatropous with the micropyle close to the placenta, and the latter author says the micropyle is below the raphe, while the former gives the length of the ovule, chalaza to micropyle, as 0·35 mm. at the time of fertilization. All three authors agree on the final shape of the embryo sac: in Tulasne's words it 'is at first elongated and blunt at both ends, but later its apex swells out to form a head which joins the body of the sac by a sort of collar'. There is, however, disagreement as to what immediately surrounds the embryo sac at time of fertilization. Tulasne might give the impression that he believed it to be the nucellus, for having just described mature ovules he says 'the...integument of these ovules...encloses a lanceolate nucellus...; this nucellus...encloses the embryo sac for the benefit of which its parenchyma is...absorbed'. He then continues by describing the swelling out of the head of the embryo sac to give the latter its final shape. Later he writes: 'before this body [meaning the embryo] has started to form,...a characteristic tunic of cells has taken the place of the nucellus.' He, probably, was not in a position to be definite about the exact time when the nucellus gives way to the 'tunic of cells', but it seems possible that the sequence of his description was at the root of Chatin's statement that 'after fertilization, of which M. Tulasne has given us all the details, this cavity [the embryo sac] grows, the nucellus disappears in front of its progress, and soon one sees nothing round it but an envelope formed by the integument'. Schmid had the truth of the matter, as will be confirmed in the body of this research, for he figures round the mature embryo sac a layer of cells (Tulasne's characteristic tunic) which he states is differentiated early from the rest of the integument. He called this layer of cells the tapetum, and some workers are still using the term. It would, however, seem better, since the homologies of the angiosperm ovule are better understood now, to follow Goebel (1905) as Carlson & Stuart (1936) have done and call it the epithelium.

III. METHODS

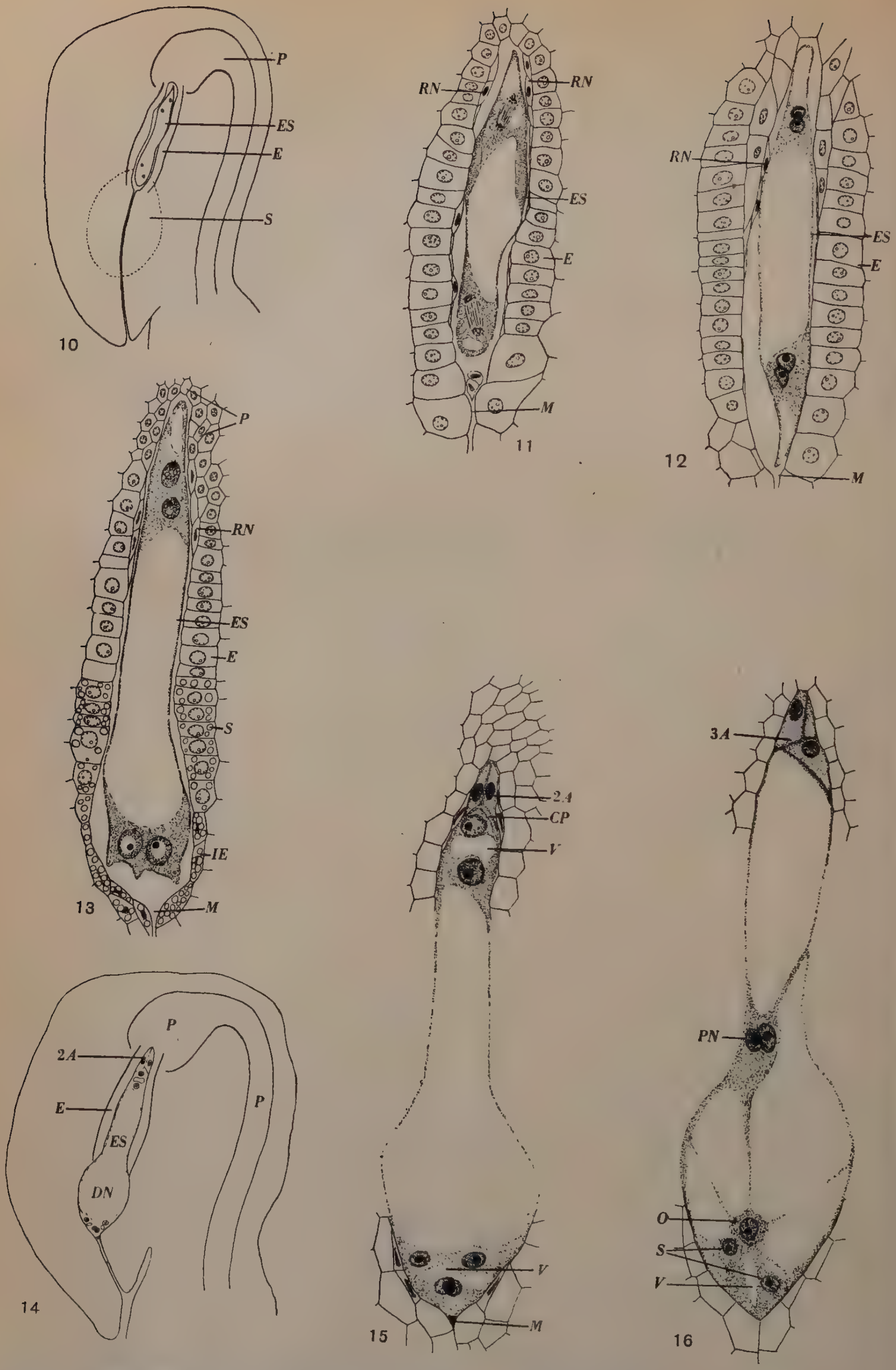
Ovaries were removed in suitable stages of development from plants growing naturally, and opened up, if they were small by a razor cut top and bottom, or if they were large by stripping off the whole ovary wall. They were then dropped into fixative of which several kinds were tried including formalin-acetic-alcohol, Carnoy, Flemming's solution and several of its modifications. None was found which did not result in some shrinkage of embryo sacs in the later stages of development. The first named yielded results as good as any other and was used for most of the material on account of its convenience in the field. Sections of wax-embedded ovaries were cut 10μ thick for the younger stages and somewhat thicker for the older ones. Staining was carried out with iron alum haematoxylin, and also with gentian violet according to La Cour's (1931) schedule. Microscopic measurements of various parts of the ovule were made, originally as a check on the sequence of development, and these are used in building up a picture of the process.

IV. STRUCTURAL CHANGES DURING THE DEVELOPMENT OF THE OVULE

The youngest ovules examined were in ovaries with a basal diameter of approximately 3 mm. The ovules were already anatropous and were fairly widely spaced over the placenta. Most were orientated so that the body of the ovule was above the funicle, but in the lower part of the ovary some had the reverse of this orientation, a fact which Chatin (1874) did not note. At this stage (Fig. 1) the ovule is broader than it is long and contains one large spore mother cell (Fig. 2) surrounded, except at the chalazal end, by a nucellus consisting of one layer of cells recognizable by their prominent nuclei. Outside this there is a single integument, four or five cell layers thick, which is already bulging around the tip of the nucellus for the formation of the micropyle. Cell divisions indicate that at this time growth is also pronounced in the raphe on a level with the tip of the nucellus. While the lips of the micropyle are closing in (Fig. 3) the region of pronounced growth in the raphe moves down into the funicle, and the latter as a result elongates to become, in many instances, longer than the body of the ovule. This continues to grow meanwhile, mainly by the elongation of the integument around the micropyle, while the spore mother cell divides (Fig. 4) to produce a linear tetrad of megaspores (Fig. 5). By the time the megaspores are delimited the nucellus stains less heavily than previously, while the inner epidermis of the integument stains more so. The epithelium, which thus becomes obvious, appears to form a cylinder, fading away at the micropylar end into the general integumental cells of that region and opening at the chalazal end into the upper part of a procambium which is, at this time, clearly marked in the raphe though visible, in some measure, from the earliest stages.

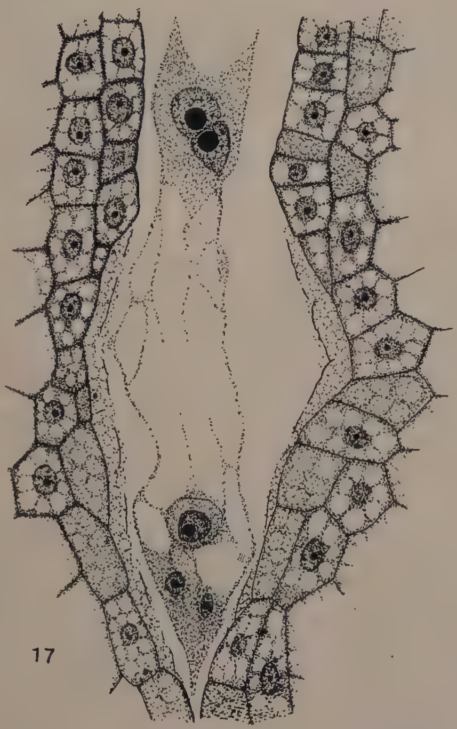


Figs. 1–9. Stages in the development of the ovule up to the binucleate condition of the embryo sac. For full description see text. Figs. 1, 3, 5 and 7 × 235 approx. Figs. 2, 4, 6, 8 and 9 × 645 approx. *N* = nucellus; *SMC* = spore mother cell; *I* = integument; *M* = micropyle; *DSMC* = divisions in spore mother cell; *4S* = four spores; *CM* = chalazal megaspore; *3AM* = three aborting megaspores; *P* = procambial strand; *E* = epithelium; *PEC* = primary embryo-sac cell; *V* = vacuole; *ES* = embryo sac; *S* = starch.



Figs. 10–16. Later stages in the development of the ovule. For full description see text. Figs. 10 and 14 × 206 approx. Figs. 11, 12, 13, 15 and 16 × 562 approx. *P* = procambial strand; *RN* = residue of nucellus; *IE* = inner epidermis of integument; *2A* = first two antipodal cells; *DN* = dilatation; *CP* = cleavage plane; *3A* = three antipodal cells; *PN* = polar nuclei. Other labels as in figs. 1–9.

The chalazal megaspore gives rise to the embryo sac, and as it grows in the process towards the micropyle there is progressive disorganization, first of the contiguous megaspore, then of the other two (Fig. 6), of the nucellus and finally of the integumental cells at the inner end of the micropyle. Here, about the time of germination of the megaspore, the cells become crowded with starch (Fig. 7). None was found in the contiguous cells of the nucellus. As the unsuccessful megaspores become disorganized in front of the enlarging primary embryo-sac cell, vacuoles become increasingly apparent in the latter (Fig. 6), but by the time its nucleus is in metaphase (Fig. 8) they have disappeared. Vacuolation is again apparent as the products of the first nuclear division separate (Fig. 9), mainly, though not entirely, as one large vacuole between the two nuclei. By this time the micropylar end of the young embryo sac is getting broader and is crushing the nucellus around it, a process which is progressive towards the chalaza as the embryo sac elongates during the remainder of the binucleate phase and until four nuclei have been formed (Figs. 10–12). Then the micropylar end of the sac begins to force its way into the micropylar canal, around which the accumulation of starch is now greater. While the embryo sac is still in the tetranucleate condition its micropylar end starts to dilate (Fig. 13), compressing the contiguous cells of the inner integumental epidermis. The chalazal end of the sac has meanwhile extended beyond the recognizable limits of the nucellus, of which little now remains even at the chalazal end, into the procambium. The process of dilatation continues during the third nuclear division, so that, by the time eight nuclei have been formed (Figs. 14, 15), the embryo sac approaches its characteristic shape.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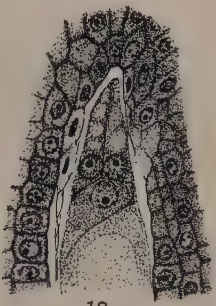
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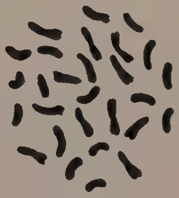
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Fig. 17. Micropylar part of embryo sac just before fusion of polar nuclei. × 800 approx. Fig. 18. Antipodal cells at similar time. × 750 approx. Fig. 19. Metaphase of last embryo-sac division. × 4000 approx.

Organization of cells in the embryo sac is initiated at the chalazal end, the two extreme antipodal cells, occupying that part of the embryo sac which has recently forced its way into the chalaza, being marked out first (Fig. 15). Moreover, the manner of separation of the three antipodal cells seems to differ from that of the other embryo-sac contents. At the chalazal end, planes of demarcation are first visible as denser lines in the cytoplasm separating the two extreme nuclei from one another and from the rest of the sac. These lines become more definite until they are recognizable as cleavage planes. On the other hand, soon after the first two antipodals are so delimited, a vacuole is apparent between the two nuclei still free at the chalazal end, and two others may be seen to the micropylar side of the two inner nuclei of the four at the micropylar end. Other vacuoles appear later (Fig. 16), among them one which separates the extreme micropylar pair of nuclei. Thus the polar nuclei and the cells of the egg apparatus seem to be separated from the antipodals and from one another by vacuolation.

While the antipodal cells (Fig. 18) and the egg apparatus (Fig. 17) are continuing their pre-fertilization development and the polar nuclei are migrating to fuse, the starch-containing cells of the integument around the micropyle suffer further crushing and disorganization, and so provide room for continued dilatation of the head of the embryo sac.

V. Dimensional changes during the development of the ovule

(a) *Validity of statements*

Table 1 sets out the means, to the nearest micron, and the probable errors of the means of measurements taken of the ovule, in a succession of easily recognizable conditions, from a large number of preparations made during the structural studies. As is apparent from the table the number of measurements made at any one stage is insufficient to allow the means to be considered as closely dependable characteristics of the various conditions of the ovule. To obtain such completely dependable means, sections of an inordinate number of ovules would be required, since only one section of many will pass near enough the axial line of the ovule to warrant measurement. The table, however, supplies a number of actual measurements which it is impossible to give in any other manner.

Despite the fact that the means cannot be regarded as completely dependable and hence small differences between means cannot be considered significant, it is believed that Fig. 20, which is constructed from the data in the table, may be interpreted on broad lines to assist in visualizing the general trend of dimensional changes during the development of the ovule. This belief is supported by the agreement between deductions drawn from the graph and those which result from direct examination of sections. In the figure, dimensions of the internal parts are plotted against ovule length as a substitute for plotting against time all dimensions of ovules grown under constant conditions, which it is not possible to obtain since constancy would necessarily apply to conditions internal to the plant, such as food supply to the ovule. Because, however, it is probable that total magnitude of the ovule varies with time, in the manner of growth processes generally, to give a sigmoid curve, the compromise made in plotting against ovule length presumably results in the graph distances between the middle stages of ovule development being longer than they would have been had a true time scale been practicable.

(b) *Interpretation of Fig.* 20

The graphs start at a stage in development where the nucellus is just invested laterally by the integument, and for a time while this is closing round the tip of the nucellus to form the micropyle, little dimensional change is indicated in the internal parts of the ovule. The slight decrease in the nucellus breadth indicated by the graph is, however, continued, and there can be little doubt that the nucellus is narrower when three spores are aborting than it is when it is still projecting from the integument. Similarly, the slight diminution in the breadth of the contents of the nucellus indicated in the graph between the formation of the micropyle and the formation of four spores is continued till when three spores are aborting there can be no doubt that they also have become narrower. The length of the

TABLE 1. *Mean dimensions of parts of ovule*

Stage and no. of observations	Ovule body length	Nucellus		Megaspore mother cell and spores		Primary embryo-sac cell		Embryo sac		
								Length	Breadth	
		Length	Breadth	Length	Breadth	Length	Breadth		Body	Head
Nucellus still projecting (13)	113 ± 1·45	83 ± 1·16	21 ± 0·21	54 ± 0·68	11 ± 0·30	—	—	—	—	—
Micropyle formed (6)	142 ± 1·62	83 ± 0·84	20 ± 0·28	54 ± 0·99	11 ± 0·39	—	—	—	—	—
Four spores (9)	192 ± 3·15	91 ± 1·95	19 ± 0·32	56 ± 0·84	10 ± 0·30	—	—	—	—	—
Three spores aborting (10)	212 ± 3·25	107 ± 2·11	18 ± 0·27	—	—	30 ± 0·53	8 ± 0·22	—	—	—
Primary embryo-sac cell vacuolating (13)	233 ± 2·52	108 ± 0·85	19 ± 0·13	—	—	51 ± 0·57	15 ± 0·12	—	—	—
Binucleate embryo sac (14)	247 ± 3·81	110 ± 0·10	18 ± 0·12	—	—	—	—	68 ± 0·26	16 ± 0·32	—
Tetranucleate embryo sac (19)	270 ± 1·57	—	—	—	—	—	—	119 ± 1·87	18 ± 0·25	27 ± 0·34
Octonucleate embryo sac (10)	265 ± 2·65	—	—	—	—	—	—	143 ± 1·60	20 ± 0·33	37 ± 0·80
Polar nuclei migrating (19)	274 ± 1·79	—	—	—	—	—	—	155 ± 1·51	20 ± 0·29	38 ± 1·16
Polar nuclei fused (13)	305 ± 2·40	—	—	—	—	—	—	181 ± 2·01	21 ± 0·26	40 ± 0·78

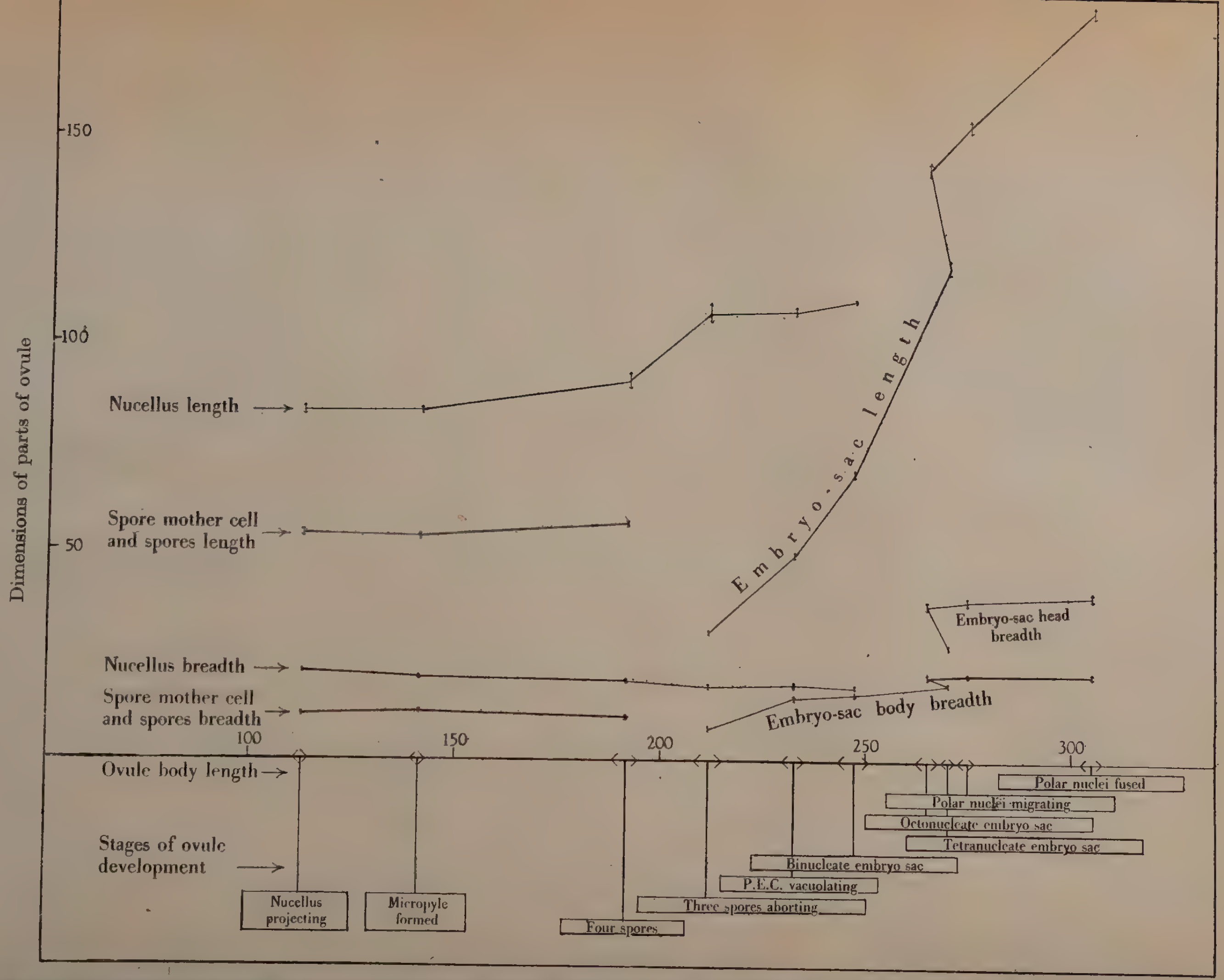

Fig. 20. Spatial and structural development of the ovule in relation to ovule size. In the bottom part of the figure rectangles enclosing

contents of the nucellus does not change greatly till after megaspore abortion sets in, though it is just possible that some elongation occurs during the formation of the four spores from the spore mother cell. Elongation of the nucellus itself between the completion of the micropyle and the spore abortion is unquestionably indicated, and this elongation, together with the simultaneous diminution in breadth, is what might be expected did the integument press inwards as its cells matured after forming the micropyle. Sections of ovules support this possibility: transverse sections show integumental cells tangentially elongated, indicating circumferential tension, and longitudinal ones (Figs. 3, 5 and 7) show a tapering tip to the nucellus drawn out by the in-squeezing integument. This squeezing is apparently effective not only on the nucellus but on its content as well, for by the time three spores are aborting the primary embryo-sac mother cell, though by now about twice as long as it was originally, about half the maximum length of the spore mother cell, gives transverse measurements only some three-quarters as great as those given by the four spores and the spore mother cell.

It is only concomitant with vacuolation that the primary embryo-sac mother cell recovers its breadth, and the process seems to be a rapid one till the transverse dimensions of the nucellus are approached, that is, while the nucellus is being crushed and till the embryo sac comes to press more or less directly on the inside of the epithelium lining the inside of the integument. Just after the three spores have aborted, growth in length of the nucellus slows down. Growth in length of the embryo sac, on the other hand, from that time on is rapid, becoming increasingly so with multiplication of the haploid nuclei within it, and by the time the tetranucleate condition is reached the embryo sac has eliminated the aborting spores and the nucellus throughout its length. In contrast to growth in length, growth in breadth of the embryo sac falls off till the micropylar end of the tetranucleate sac has escaped from the epithelium into the micropylar canal, when dilatation for the formation of the embryo-sac head begins at a rate which is rapid until the octonucleate stage. That this dilatation takes place at the expense of some of the cells of the integument has been indicated under structural changes, but from the measurements one may perhaps deduce a possibility that part of the space necessary to accommodate the dilation may result from distortion of the residual mass of integumental cells around it. The table of mean dimensions shows the ovule to be shorter in the octonucleate stage than it is in the tetranucleate one, and such a contraction in the length of the ovule might reasonably be ascribed to the forces of expansion within the embryo sac being partly expended in stretching the micropylar region of the ovule laterally, so inducing a correlative contraction along its length. With so few measurements as have been taken, giving means for the three stages centered on the tetranucleate sac so close together, there can, however, be no certainty in this.

With the approach together and the fusion of the polar nuclei, growth of the embryo sac slows down. The graphs of embryo-sac body and head breadths are now almost horizontal, and the inclination of the line for length of the embryo sac at 45° indicates that elongation of the embryo sac is taking place now only at the same rate as it is occurring in the ovule as a whole. It would thus seem as if the establishment of diploid conditions within the embryo sac eliminated whatever advantage this previously completely haploid structure employed to the detriment of the diploid tissue around.

There thus appear to be three dimensional phases in the development of the ovule. During the first, the still rapidly growing integument moulds the older nucellus and its contents in a manner which tends to their elimination. The second phase is initiated in the vacuolation of the primary embryo-sac mother cell which, by this means, escapes the threatened elimination to crush the nucellus and invade the integument more and more rapidly as its haploid nuclei multiply. The third is centred round the fusion of the polar nuclei. In it what little growth of the embryo sac still goes on does so in unison with that of the rest of the ovule.

VI. Discussion

There are two ways in which the present research bears on the general problem of ovule development. These concern the time of vacuolation of the megaspore and the relative times of development of the two ends of the embryo sac.

Many general accounts of embryo-sac development emphasize the appearance of a large vacuole immediately after the first division in the embryo-sac mother cell, e.g. Schnarf (1936), but Chiarugi (1927) mentions vacuolization before this, as part of the 'Fase della mitosi somatogenica', and Maheshwari (1937) states that two vacuoles are present before the megaspore nucleus divides. Among some seventeen accounts of embryo-sac development published in the *Annals of Botany*, the *New Phytologist* and the *Botanical Gazette* subsequent to Maheshwari's paper, I can find support for his statement in four only: Bushnell (1936), Billings (1937), Popham (1938), and Goldberg (1941), and Billings qualifies his statement. From the other thirteen papers no conclusions can be drawn on this point, and one can suppose only that there is doubt or variability in the process, or, alternatively, that interest has centred on the nuclear divisions to the exclusion of other observations. This was not the case in the present research and vacuolation was seen prior to the division, though since vacuoles were not apparent during the first nuclear division, had not stages prior to that division been carefully studied, the false conclusion might have been drawn that vacuolation started after the division.

The time of inception of vacuolation may be useful in leading to an understanding of the reason why one megaspore develops while the other three abort. Darlington & La Cour (1941) suggest, on analogy with pollen development, that the viability of megaspores should vary in the same plant, and say that this variation is likely to be most serious in cases of structural hybridity and polyploidy. According to Maude (1939) in *Digitalis* $x=7$ and in *D. purpurea* $2n=56$, so this species is probably a polyploid, and if Darlington & La Cour are right there might be variability in the viability of its megaspores. I was unable to find any but chalazal megaspores developing, though there remains the possibility that competition between the chromatids of the megaspore mother cell nucleus may be a factor in deciding which chromatid out of each tetrad shall enter into the nucleus occupying the favoured position. Unless some such mechanism as this regularly separates out three non-viable micropylar megaspores, position in the ovule would seem to be the master factor determining which of the megaspores shall develop. Moreover, since vacuolation of the chalazal megaspore starts very early, while the micropylar megaspores are shrivelling, it would seem that the master factor of position resolves in part at least into conditions for producing a higher suction force in the chalazal megaspore than in its fellows. It has been noted already that, about the time when vacuolation is first apparent, numerous starch grains are to be seen in the integument around the inner end of the micropyle. They do not appear in the nucellus or within it, a condition which might be attributed, either to the presence of a starch-accumulating mechanism outside and its absence from within the surface of the nucellus, or alternatively to the action of that surface as a barrier between the region of food entry at the funicle and the megaspores. This surface is peculiar, in that it is the surface of contact formed when the nucellus is being invested by the integument, in all except its chalazal parts. Here there is the continuity of one tissue through which it may reasonably be presumed translocation occurs readily, so affording to the chalazal parts of the nucellus and its contents the opportunity of accumulating solutes earlier than the micropylar parts. Evidence that the nucellus cells nearer the micropyle have a lesser suction force than those nearer the chalaza may be deduced from the way in which the enlarging embryo sac broadens to crush that tissue near the micropyle first and then progressively towards the chalaza, since it is hardly probable that the turgor pressure would differ from within the embryo sac. And if the cells of the nucellus have a lower suction force nearer the micropyle, there seems no reason why the cells in the row of megaspores should not also.

Maheshwari (1937) states that during the formation of the normal type embryo sac the last two divisions are rapid and simultaneous, and that departures in the sequence of these divisions are usually in the nature of abnormalities. Among the three examples he gives of departure from simultaneous development is the instance of *Paulownia* reported by Millsaps in 1936, where divisions at the antipodal end of the embryo sac are precocious, and I find in the seventeen papers mentioned earlier two reports of similar precocity: Westfall (1940) figures antipodal cells of *Lilium tigrinum* walled prior to the completion of the micropylar divisions, and Popham (1938) states that the antipodal cells of *Galinsoga ciliata* are walled first. Only five of the seventeen researches state that development is simultaneous at the two ends of the sac. The remaining twelve allow no conclusions on this point, and so again one has to presume that interest has centred on other features.

I have been able to find in my material only one embryo sac in which all the final divisions are visibly in progress, and hence am not able to say whether this instance is normal or abnormal for *Digitalis purpurea*. In it the two nuclei nearer the central vacuole were in anaphase, the two at the extremities of the sac in metaphase, both showing 28 chromosomes (Fig. 19). Thus the divisions are not simultaneous, nor is there earlier division at one end of the sac than the other. On the other hand, a large number of embryo sacs were seen in which antipodal cells were delimited but cells of the egg apparatus were not, and one is inclined to ascribe to this precocity the same cause as that which leads to the megaspore at the chalazal end of the ovule developing while its fellows abort.

VII. SUMMARY

1. The young ovule of *Digitalis purpurea* has one integument four or five cells thick and a single-layered nucellus enclosing a spore mother cell from which a linear tetrad of megaspores is formed. The chalazal megaspore enlarges while three sets of nuclear divisions are occurring, crushing the three other megaspores and the nucellus so that in later stages of development an epithelium, derived from the inner epidermis of the integument, is the immediate investment of the embryo sac.

2. Antipodal cells are delimited before the cells of the egg apparatus.

3. From measurements made of the various parts of the ovule it is deduced that, until vacuolation starts in the primary embryo-sac mother cell, the integument compresses the parts within it, but that this vacuolation results in a counter pressure by which the three aborting megaspores, the nucellus and the inner part of the integument around the micropyle are crushed, the outer part of the last possibly being distorted so that the total length of the ovule becomes less.

4. The possibility is discussed that the surface of contact between the integument and the nucellus delays the passage of solutes from the integument inwards, except where they form a continuous tissue at the chalaza, thus creating in this region a priority of supply which enables the chalazal megaspore to succeed and the antipodal cells to develop precociously.

This research was carried out with apparatus purchased with a grant from the Dixon Fund.

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Typification and Variation in the Smooth-Leaved Elm, Ulmus carpinifolia Gleditsch.

By R. MELVILLE.

(With Plate 3 and 6 Text-figures)

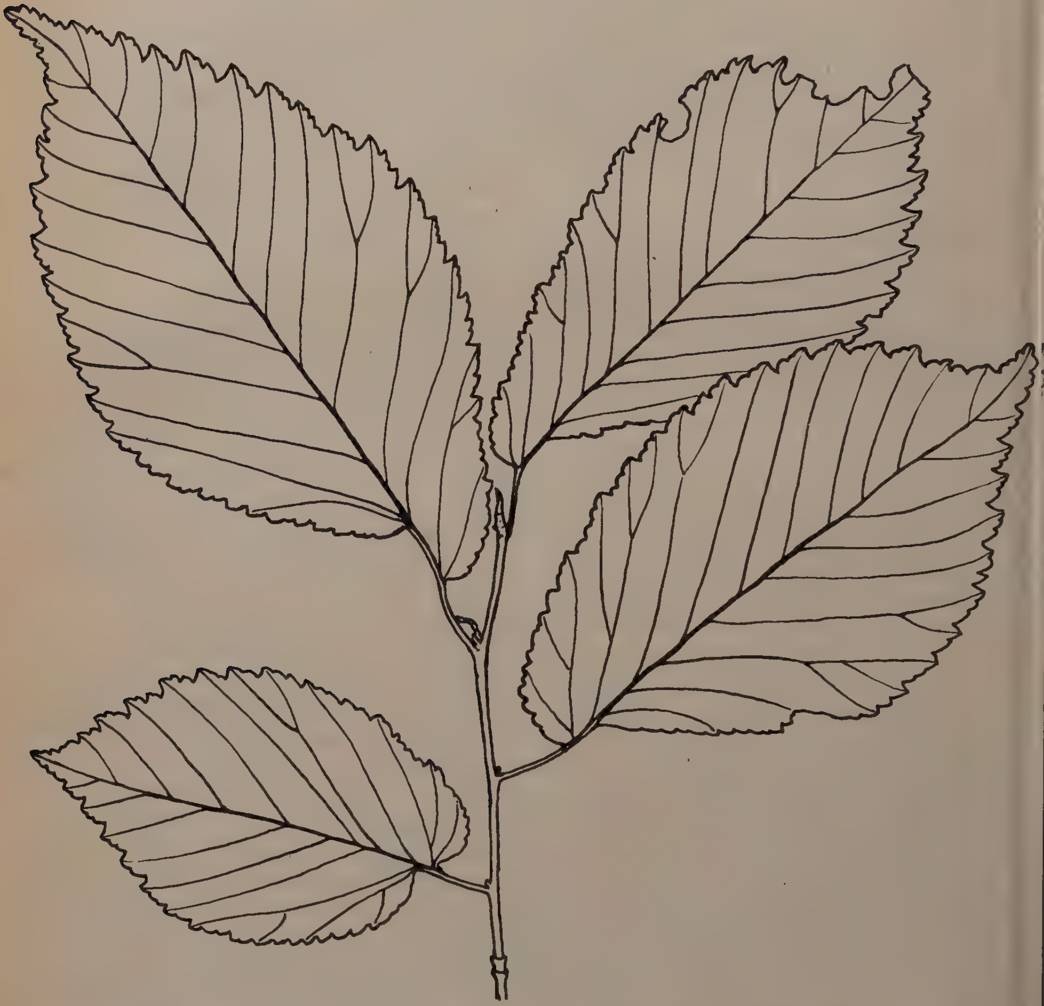
[Read 8 November 1945]

As long ago as 1633 Goodyer distinguished a smooth-leaved elm, *Ulmus folio glabro*, in his account of the elms published in Johnson's edition of Gerard's *Herbal*. Miller appears to have gathered up this with Goodyer's other three elms without adding much to our knowledge of the plant and it appears in the eighth edition of the *Gardener's Dictionary* (1768) as *U. glabra*. This name cannot be used for the species, however, as it is a later homonym of *U. glabra* Huds. (1762), the common wych elm, referred to as *U. montana* Stokes (1796) by many British authors. More recently, British botanists have used *U. nitens* Moench (Meth. 333, 1794), but this name also is invalid, since it is a renaming of a previously described species, *U. carpinifolia*.

Moench cited *U. carpinifolia* as a synonym, but gave Ehrhart as the author of the name. This was almost certainly an error, as the name does not appear in any known work of Ehrhart. The true authorship of the name was traced by Rehder (*J. Arnold Arbor.* XIX, 266, 1938) to Gleditsch, who published it in his rare and little known work, *Pflanzenverzeichniss* (p. 354, 1773). Among other names that have been widely applied to this species are *U. foliacea* Gilibert (*Exerc. Phytol.* II, 395, 1792), and *U. campestris* L. In his preface Gilibert stated that he had repudiated certain names that appeared inappropriate to him, and among these was *U. campestris* L., so that *U. foliacea* Gilibert was superfluous and invalid. Although the Linnaean name has been widely used on the continent of Europe for this species, the variety of interpretations that have been placed on it have rendered its application ambiguous; the case for the rejection of *U. campestris* L. as a *nomen ambiguum* has been published already (Melville, *J. Bot., Lond.*, LXXVI, 261–5, 1938).

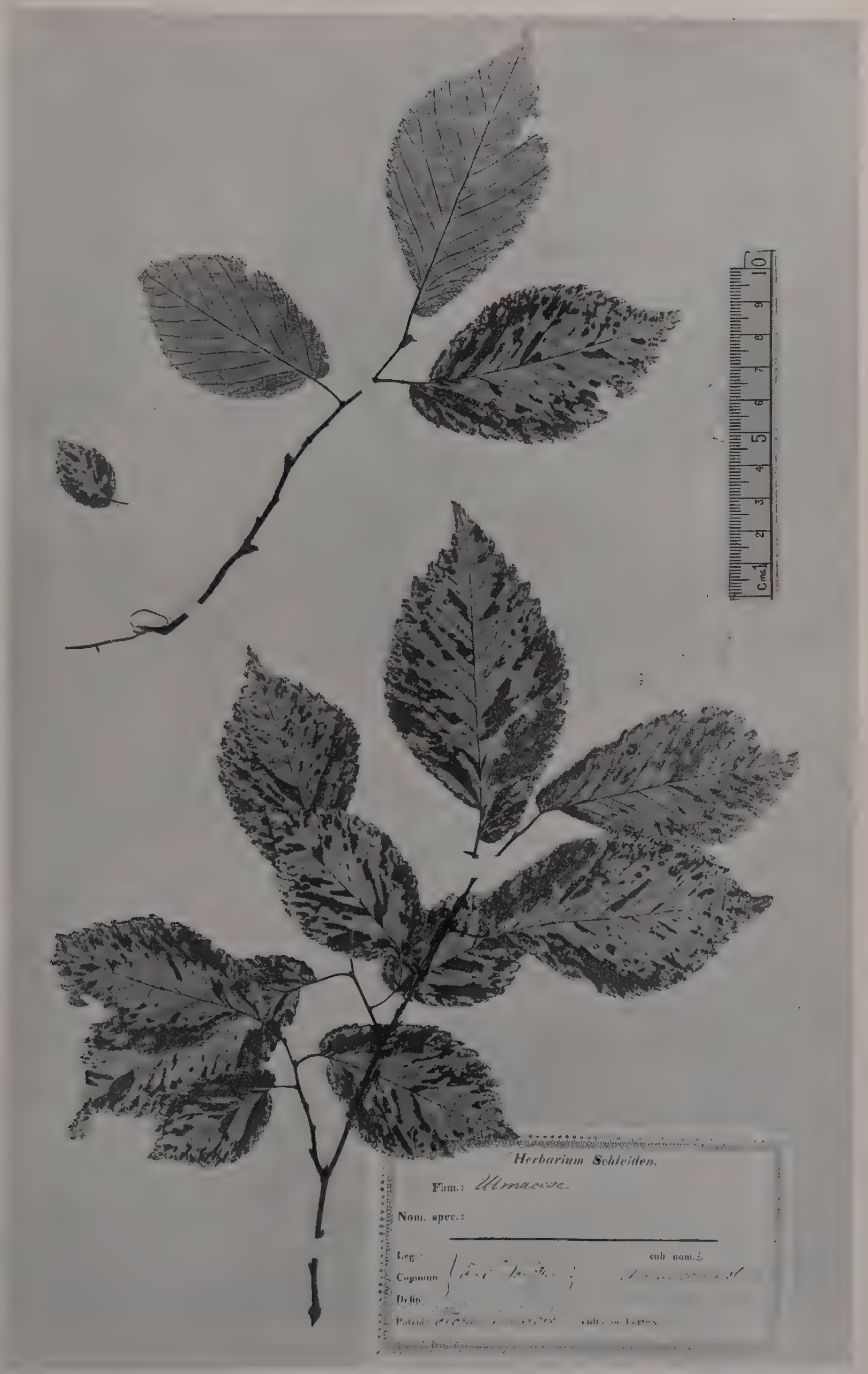
There is no reason to doubt that Miller, Moench, Gleditsch and Gilibert were all describing a smooth-leaved elm. It is not equally clear that they were all describing the same elm. If they were, then *U. carpinifolia* Gled. is the correct name to use for it, but there is room for doubt whether Miller had in mind the same tree as the continental authors. Had a specimen from either of these authors survived it would have helped to settle this question. *U. glabra* is not now represented in the Miller Herbarium at the British Museum, and when Moss made inquiries as to the existence of a type of *U. nitens* Moench (*Gard. Chron.* Ser. 3, LI, 217, 1912) he was informed by Prof. L. Diels that he believed that Moench's specimens had been destroyed. I am unaware of the survival of a Gilibert type, if, indeed, one ever existed, since it would not have appeared important to that author to keep a specimen when he was merely changing the Linnaean name. The position is somewhat similar in the case of Gleditsch, who, according to Rehder (loc. cit.), based *U. carpinifolia* on the '*Ulmus carpini folio seu cortice arboris albido*' of Ruppius (*Fl. Jena*, ed. Haller, p. 330, 1745), 'as is clearly shown by the citation under *Ulmus carpini folio* in Gleditsch, *Syst. Einleit. Forstwiss.* I, 240, 1775'.

In the absence of a type specimen, the question of the type locality must be considered. On the evidence of the above quotations there is strong justification for considering the Jena area as the *locus typicus*. Accordingly, an attempt was made to obtain fresh material from the Jena neighbourhood. By the courtesy of Sir A. W. Hill a request for specimens was sent in 1938 to Dr O. Renner, Director of the Botanic Garden of the Friedrich-Schiller University at Jena. I am much indebted to Dr Renner and to Prof. Dr Th. Herzog of the Friedrich-Schiller University for the efforts they made to obtain local material of *U. carpinifolia*. Unfortunately, all they were able to collect from the botanic garden and from wild stations proved to be forms of the hybrid *U. glabra* Huds. × *carpinifolia*. In some of these the leaf shape approximated to that of *U. carpinifolia* but the leaves were larger and scabridly hairy, while other features of the twigs and buds combined to indicate a hybrid origin. Prof. Herzog also sent on loan from the Schleiden Herbarium a specimen which undoubtedly belongs to *U. carpinifolia*. Unfortunately, it is a variegated form, a circumstance which may tend to cast doubt on its status as a wild plant. However, variegated sports of many plants occur wild, and I have myself found a variegated form of the smooth-leaved elm growing wild in Essex. Furthermore, variegated elms not infrequently revert to type and both kinds of foliage may be found together on the same tree. Little importance, therefore, need be attached to this character.



Text-fig. 1. A short shoot from the neotype of *Ulmus carpinifolia* Gleditsch. (Natural size.)

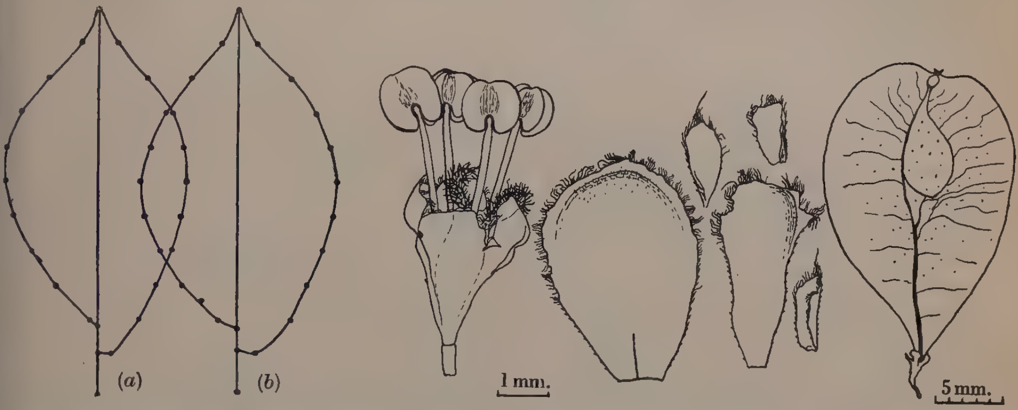
In his letter, Prof. Herzog states that the specimen was collected wild in the Jena neighbourhood in a small wood at Gross-Lobichau cited in Bogenhard's *Flora*. He went to some trouble to locate this wood, without success, and the local forester said that it no longer exists; presumably it had long since been cut down and cleared. The flora mentioned, C. Bogenhard's *Flora von Jena*, was published at Leipzig in 1850. On p. 333 *U. campestris* L. is mentioned, a name at that time commonly in use by Continental authors for *U. carpinifolia*. Bogenhard states the local distribution as follows: 'Einzeln in Wäldern und



Photograph of the neotype of *Ulmus carpinifolia* Gleditsch in the Schleiden Herbarium, Friedrich Schiller University, Jena. (*Photo.*: G. Atkinson)

angepflanzt. Hinter Grosslöbigau ein Wäldchen davon.' The label on the Herb. Schleiden specimen gives the identification *U. campestris* in ink, below which the words 'var. *variegata*' have been written in pencil in a different hand and evidently at a later date. The specimen was collected by F. S. Voigt, the locality being stated indefinitely as 'Flora Jenensis'. The words 'culta in Horto' printed on the label are crossed out in ink, so the specimen did not come from the botanic garden. From this fact and the circumstances related above, I believe the specimen was gathered from a wild tree.

The Herb. Schleiden specimen consists of one branchlet bearing three short shoots and one separated short shoot, from normal adult branches (Plate **3** and Text-fig. 1). The date of collection is not recorded, but the leaves are little more than full grown and a few stipules remain, a stage usually reached in June. The leaves are smooth above and bear numerous glands below. The following diagnostic characters are well marked: leaf with cuneate base, the base of the long side of distal and subdistal leaves making a sharp or rounded 90° turn inwards to the petiole, serrature rather sharp with distal side of teeth concave, long petioles and slender branchlets, at one year old 1–1·5 mm. thick. All these features were in conformity with the mental picture I had formed from an examination of the rather scanty material of European elms in our national herbaria and of cultivated trees obtained from continental sources. I am satisfied that this specimen is a typical example of the continental smooth-leaved elm, and in the absence of more suitable material have chosen it as a neotype on which to base a new and critical description.



Text-fig. 2. Mean leaf shapes, flower and fruit of *Ulmus carpinifolia* Gleditsch. (*a*) Mean leaf shape of distal, (*b*) of subdistal leaves of the Herb. Schleiden specimen. Centre: flower, two bracts and three bracteoles; right: fruit, from British specimens (Essex, Melville no. 36.21).

It is not yet known whether the Schleiden Herbarium has survived the war, but good photographs of the specimen were obtained in 1938, and natural size prints are filed in the Herbarium at Kew. Drawings and measurements were also made. In the following description, vegetative characters are based mainly on the Herb. Schleiden specimen and floral and fruit characters on British material (Melville no. 36.21, Text-fig. 2) collected at Cottered Green, Essex.

Ulmus carpinifolia Gleditsch, amplified description:

An erect tree up to 30 m. high with spreading or ± ascending branches. First year branchlets of the short shoots generally 1–1·8 mm. diameter, at first with scattered glands, and few or no simple hairs except in the stipular axils, finally glabrous, shining, chestnut-brown, lenticels scattered, rounded, inconspicuous. Short shoots with 3–5 leaves, distal and subdistal leaves obovate acute, base narrowly to broadly cuneate, slightly to markedly asymmetric, margin of the long side making a sharp or rounded right angle turn before meeting the petiole, the midrib normally straight. Lamina length of distal and subdistal leaves 5–10 cm. or up to 11·5 cms.; upper surface of lamina at first with scattered minute scabrid hairs and scattered glands finally smooth and shining, lower surface at first with numerous glands and sometimes short scattered hairs, later ± smooth except for rather prominent villous axillary tufts along the midrib; main lateral nerves on the long side 9–12 or up to 14, frequently forked near the margin; margin biserrate, serrations at $\frac{1}{3}$ lamina length from the apex usually acute with the distal edge concave and proximal edge with 1–3 subsidiary teeth; petiole 9–15 mm. long, pubescent above, glabrous below. (For co-ordinates of mean leaf shapes, see below.) Basal leaves of short shoots ovate to lanceolate acute. Stipules caducous, lanceolate to linear, 8–14 mm. long, 1–4 mm. broad, with numerous scattered glands. Long shoots with more numerous leaves similar to the subdistal leaves of short shoots. Vegetative buds ovate acute 2·5–5 mm. long, bud scales 4–5 imbricate, short ciliate, minutely scabrid. Flower buds, ovate, bracts obovate, cuneate to narrow cuneate, fringed with simple hairs and occasional stipitate glands; bracteoles oblanceolate to blunt oblong, ciliate, often with a scabrid keel. Flowers 15–35 together, perianth funnel-shaped, cut $\frac{1}{3}$–$\frac{1}{2}$ its length in 4–6 ciliate lobes, stamens 4 or 2–3, ovary included. Fruit 13–23 mm. long, 8–13 mm. broad, broadly to narrowly obovate, apex rounded, base cuneate, centre of seed $\frac{1}{3}$ from the apex, surface with scattered glands, often coloured red over the seed. Stigmatic notch closed, the arms overlapping. Seedling with all leaves of first year's growth in opposite pairs.

The mean leaf shapes of distal and subdistal leaves of typical short shoots are shown in fig. 2*a* and *b*. The coordinates from which these are plotted were obtained by a method already described (Melville, *Ann. Bot.*, *Lond.*, N.S. I, 673, 1937), all the available leaves (4) of the Herb. Schleiden specimen being measured. The measurements are given in order from base to tip, stated as percentages of the lamina length.

Herb. Schleiden specimen, distal leaves of short shoots:

Short side: 8·5/0, 10/2·0, 20/12, 30/19, 40/24, 50/26, 60/26, 70/22, 80/14, 90/5·0, 100/0.
Long side: 0·3/0, 0/3·8, 10/12, 20/17, 30/21, 40/24, 50/25, 60/25, 70/21, 80/14, 90/5·8, 100/0.
Petiolar ratio 12; mean length of lamina 8·5 cm.; mean no. of lateral nerves, long side 12.

Herb. Schleiden specimen, subdistal leaves of short shoots:

Short side: 7·5/0, 10/5·5, 20/16, 30/23, 40/27, 50/27, 60/25, 70/21, 80/13, 90/4·8, 100/0.
Long side: 1·5/0, 0/5·3, 10/16, 20/20, 30/25, 40/28, 50/29, 60/27, 70/23, 80/16, 90/5·5, 100/0.
Petiolar ratio 13; mean length of lamina 8·7 cm.; mean no. of lateral nerves, long side 13.

Many of the British elms assigned by earlier authors to the smooth-leaved elm cannot be embraced in *U. carpinifolia* as here defined. There is reason to doubt the identity of Smith and Sowerby's figure (T. 2248) in *English Botany* as the twisting of the leaves by the artist obscures their true form. However, the specimen of *U. glabra* Mill. in Smith's herbarium in possession of the Linnean Society, collected in Essex by G. Forster in June 1810, on which the figure is said to be based, is *U. carpinifolia*. Another specimen, said to be from the same tree 'near Chingford', in the Borrer Herbarium at Kew, is also *U. carpinifolia*. On the other hand, a second specimen in Herb. Borrer collected by Forster is not *U. carpinifolia* and is more like the figure T. 2248 to which it is referred on the label. Herb. Borrer also includes a sheet of *U. glabra* Mill. var. *glandulosa* Lindley, which matches the varietal type in the Lindley herbarium at Cambridge, described by Lindley in 1829 (*Syn. Brit. Fl.* 226) from a tree on the Castle Terrace at Ludlow, Shropshire. This must now be called *U. carpinifolia* var. *glandulosa*. On visiting the locality in 1939 with H. K. Airy-Shaw, we found a single tree with identical foliage. The tree had been pollarded some years previously, but appeared to be old enough to have been sampled by Lindley. It is a good form of *U. carpinifolia* and is here used as a standard for comparing variation within the species (Text-fig. 3). The mean co-ordinates for the leaf shapes based on ten leaves are as follows:

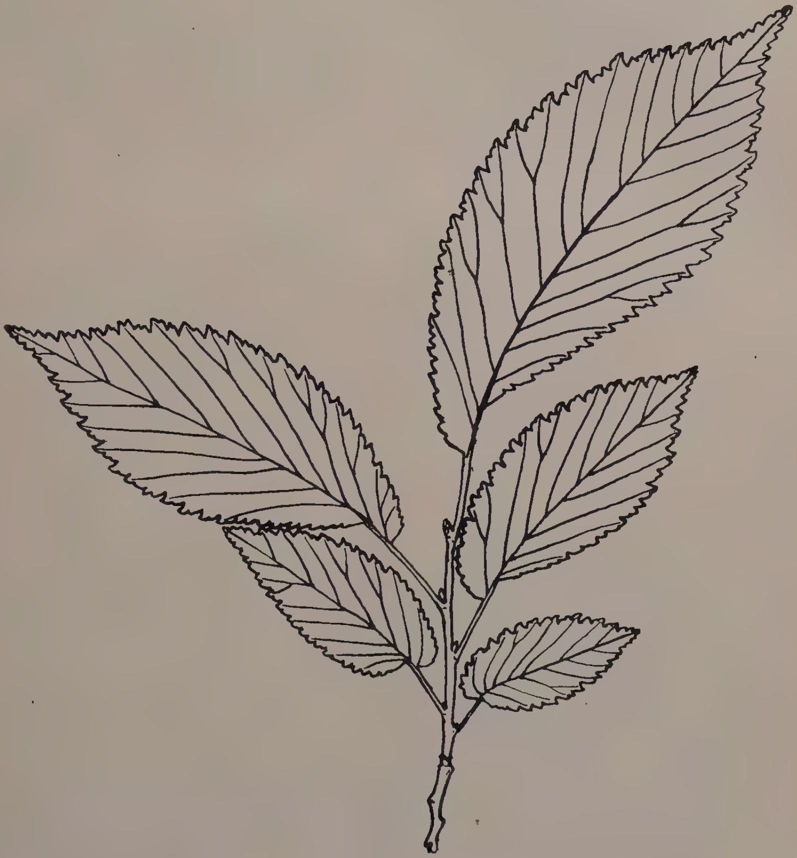
Ludlow elm, No. 39.62, distal leaves of short shoots:

Short side: 8/0, 10/2, 20/9, 30/15, 40/20, 50/22, 60/21, 70/19, 80/14, 90/4·9, 100/0.
Long side: 0·5/0, 0/2·4, 10/9, 20/15, 30/20, 40/23, 50/24, 60/23, 70/19, 80/12, 90/4·3, 100/0.
Petiolar ratio 14; mean length of lamina 7·3 cm.; mean no. of lateral nerves, long side 11.

Ludlow elm, No. 39.62, subdistal leaves of short shoots:

Short side: 8/0, 10/3, 20/11, 30/17, 40/21, 50/23, 60/22, 70/19, 80/12, 90/4·7, 100/0.
Long side: 0·4/0, 0/3·4, 10/12, 20/18, 30/22, 40/25, 50/26, 60/24, 70/21, 80/15, 90/5·0, 100/0.
Petiolar ratio 16; mean length of lamina 5·5 cm.; mean no. of lateral nerves, long side 10.

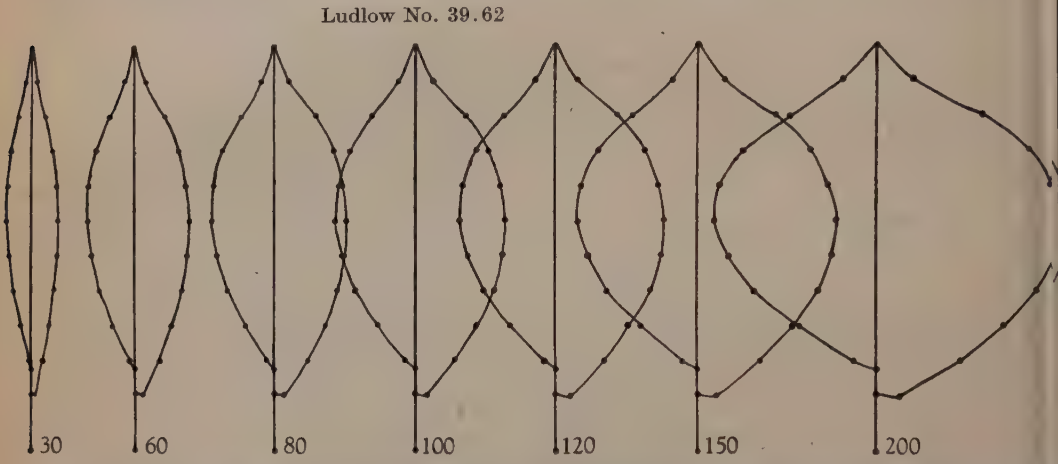
Leaves of the Ludlow tree differ from those of the Herb. Schleiden specimen in minor details only. They are slightly smaller, relatively narrower and the base of the long side is more slender. The Ludlow tree is typical of the species as represented in Britain, but there is no evidence that it is native in Shropshire or the western counties. Outside of East Anglia and the Home Counties it appears sporadically as isolated trees or groups of a few individuals. Often these are obviously planted. In the eastern counties *U. carpinifolia* is more frequent and hybrids of it with *U. glabra* Huds. are not uncommon. Many of these are planted and come under suspicion as importations from the Continent, for it is known that elm seedlings have been imported in considerable numbers for the past three hundred years or more. Although it seems likely that *U. carpinifolia* is native in the area east of the Fens extending from Norfolk to the Thames estuary, further field work will be necessary before this can be satisfactorily established.



Text-fig. 3. A short shoot from the Ludlow tree (Melville no. 39.62) believed to be the type tree of Lindley's *Ulmus glabra* Mill. var. *glandulosa*. (Natural size.)

The examination of a large number of individuals of *U. carpinifolia* has brought to light two principal kinds of variation within the species. One is a simple variation in leaf breadth similar to that reported for *U. glabra* Huds. by Lindquist (*Rep. B.E.C.* 1931, IX, 785, 1932) and for *U. stricta* Lindl. by Melville (*Proc. Linn. Soc.* CLI, 152, 1939). A series of leaf shapes varying only in breadth may readily be calculated from the co-ordinates determined for the mean leaf shapes recorded above. It is convenient to use for this purpose the subdistal leaf of the Ludlow tree. A suitable series (Text-fig. 4) is obtained by taking 30, 60, 80, 120, 150 and 200 % of each co-ordinate of breadth along the leaf. The resulting shapes form part of an arithmetic series and reproduce very closely the kind of variation observed in nature. The 120 % member is very similar to the Herb. Schleiden and other continental specimens. There is an indication that breadths equalling the 150 % member may be attained and in the other direction shapes as narrow as 60 %. The latter limit is reached in an elm cultivated at Åkarp near Malmö in Sweden under the name *U. campestris* var. *Horsholmii* Hort. This form is reputed to be of Danish origin.

The occurrence of such a narrow-leaved form in Sweden, broader forms in Britain and still broader forms in southern Germany and elsewhere is suggestive of the existence of a geographical cline or topocline for the character of leaf shape. The direction of increasing breadth appears to be roughly from north to south as in *U. glabra* Huds., but more details of the distribution of the continental forms are needed for confirmation.



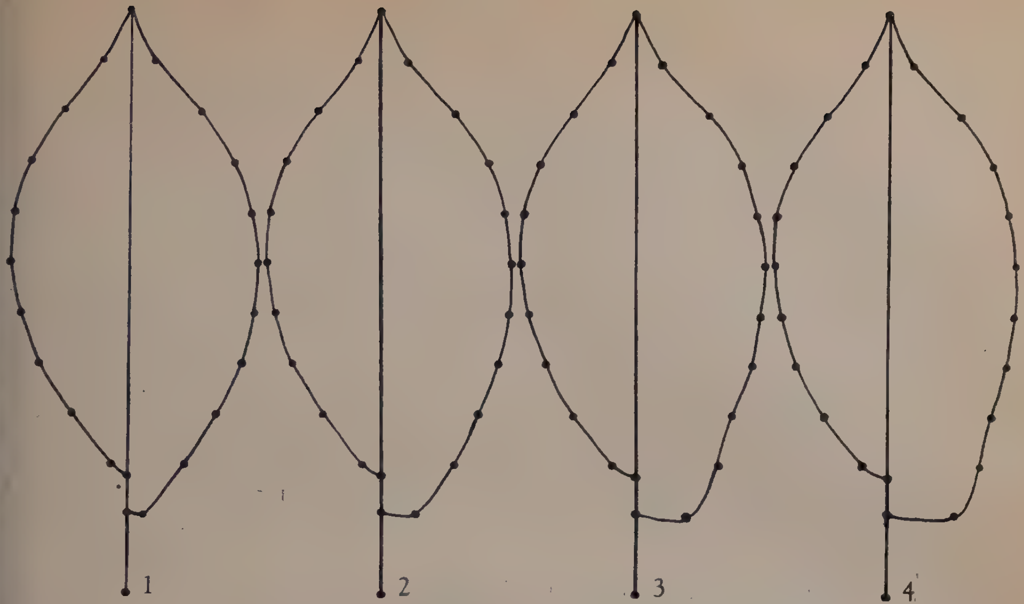
Text-fig. 4. Calculated leaf shapes forming part of an arithmetical series differing only in breadth. The series is based upon the mean shape of subdistal leaves of short shoots of the Ludlow tree, *Ulmus carpinifolia* Gleditsch var. *glandulosa* (Lindl.). The numerals indicate percentage breadths.

In the second kind of variation the base of the long side of the leaf varies in breadth independently of the breadth of the distal half of the leaf. Whereas a simple variation in breadth along the whole of the length of the lamina can be explained by a uniform change in the rate of growth at all points from base to apex, in the broad-based forms there must be a decrease in the rate of growth in breadth from base to apex. The decrease is so rapid that no difference can be detected in the shape of the distal half of the leaf compared with the normal type. Such a result would occur if the growth rates at different points along the lamina formed a logarithmic series. An attempt was therefore made to calculate a series of logarithmic transformations from the data of the Ludlow tree.

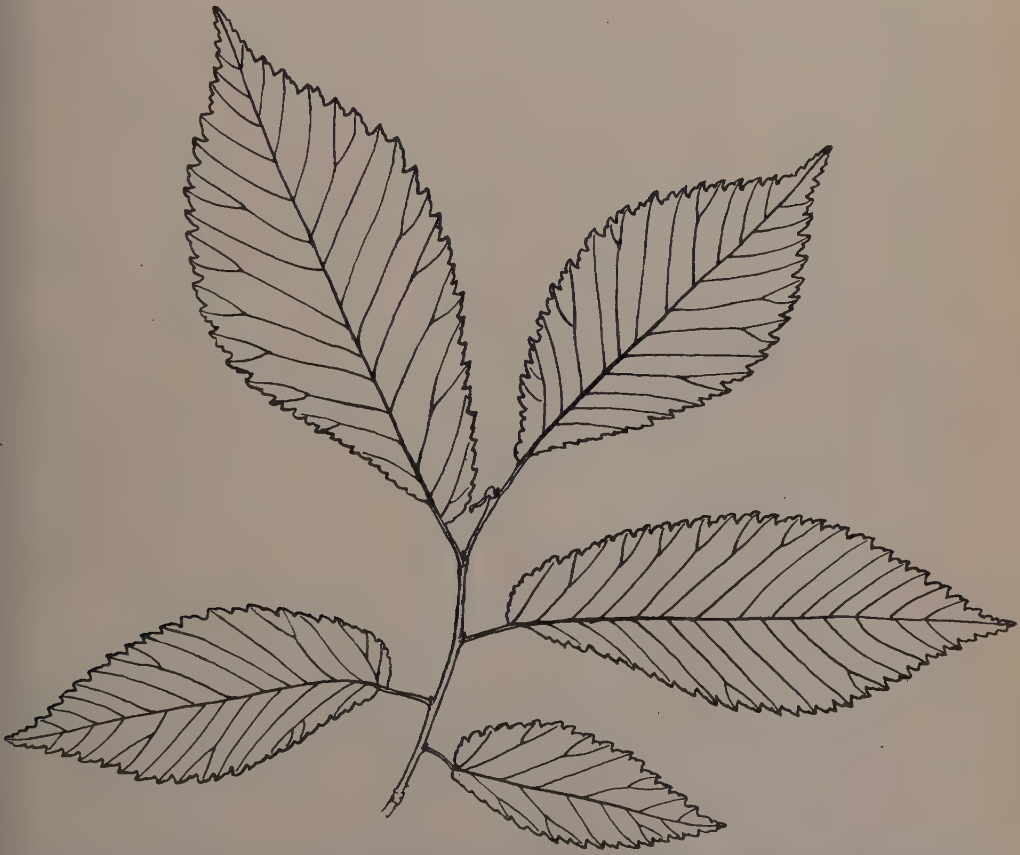
The factors necessary to convert the observed co-ordinates were obtained by application of the formula:

$$\log Fn = A^{n-1} \log F_1.$$

It was found by trial that $\frac{1}{3}$ was a suitable value for the constant A, while the basal factor F_1 is the number of times broader than the Ludlow specimen the base is required to be. The factors for the co-ordinates at each 10 % level along the leaf were found, therefore, by the simple process of dividing the log of the basal factor successively by 3.



Text-fig. 5. A theoretical series of leaf shapes based on subdistal leaves of the Ludlow tree (1) obtained by multiplying the co-ordinates of breadth by a factor which decreased logarithmically from base to apex. The numerals are the basal factors.



Text-fig. 6. A short shoot from a tree of *Ulmus carpinifolia* Gleditsch var. *suberosa* (Moench) Rehd. growing in the arboretum, Royal Botanic Gardens, Kew (Arboretum no. 183). (Slightly reduced.)

After the fourth member in the series the factor was too small to cause any visible change of shape, so that the upper half of the leaf remained unaltered. The shapes derived by the use of basal factors of 2, 3 and 4 are shown in Text-fig. 5. The effect on the short side of the leaf is inconsiderable as it tapers to the base and begins higher up the midrib.

The factor 2 produces a leaf base similar in width to that of the Herb. Schleiden specimen. The much broader base produced by a factor of 3 gives a shape almost identical with that of leaves of Kew trees of the variety *suberosa* (Moench) Rehd. (Text-fig. 6). A point of some interest is the occurrence of a slight inflexion of the margin on the long side about one-fifth the lamina length from the base. This could be smoothed out by a slight alteration in the constant A in the formula, but reference to the specimens shows that a similar inflexion is found in a proportion of the leaves of trees that have broad-based leaves.

Observations suggest that inheritance of the broad leaf-base character is independent of leaf width, though necessarily there is an interaction during leaf development of several factors which results in the observed leaf forms. The natural distribution of forms with broad-based leaves is unknown at present and much more field work by Continental botanists will be necessary before our knowledge of *U. carpinifolia* is complete. I hope that this paper may serve to stimulate research into the interesting problems in taxonomy, distribution and leaf development that the elms provide.

APPENDIX

As some of the forms mentioned in this paper have not hitherto been transferred to *U. carpinifolia* Gleditsch, the following new combinations and definitions are provided:

U. carpinifolia var. **glandulosa** (Lindl.) Melville, comb.nov. (*U. glabra* Mill. var. *glandulosa* Lindley, *Syn. Brit. Fl.* 226, 1829). Distal and subdistal leaves of the short shoots narrowly obovate, acute, with greatest breadth about 45 % of the lamina length in the distal and 50 % in the subdistal leaves; basal half of margin of long side, arched or nearly straight, making a sharp rectangular turn at the base 2–4 mm. from the petiole.

U. carpinifolia var. **Horsholmii** (Hort.) Melville, comb.nov. (*U. campestris* var. *Horsholmii* Hort.). Distal and subdistal leaves of short shoots lanceolate to narrowly obovate, acuminate, with greatest breadth of distal leaves about 32 %, of subdistal leaves about 36 % of the lamina length; basal half of margin of long side arched or nearly straight, making a sharp turn at the base 2–5 mm. from the petiole. Habit pyramidal.

Arbor pyramidalis, foliis lanceolatis vel anguste obovatis acuminatis basi cuneatis.

U. carpinifolia var. **suberosa** (Moench) Rehd., in *J. Arnold Arbor.* XIX, 266, 1938. Distal and subdistal leaves of the short shoots obovate-lanceolate, acute, distal leaves with cuneate or broad base, subdistal leaves with broad base, their greatest breadth about 43 % of the lamina length; basal half of margin of long side arched, straight or concave, making on the subdistal leaves a rounded turn at the base about 6 mm. from the petiole.

New and little-known wild potato species from Bolivia and Peru.

By M. Cárdenas and J. G. Hawkes.

(With 10 Text-figures)

[Read 21 February 1946]

The taxonomy of the wild potatoes, although already dealt with in a voluminous literature, is still very far from being complete. Even along the chief routes of communication in South America that are much frequented by collectors and travellers, new forms and varieties of species are often to be met with, whilst it is certain that in the relatively unexplored areas, or even those only a small distance from the main towns, much completely new material awaits collection.

Thus, two of the species described in the present paper were taken from places as well frequented by visitors as Saxahuamán and Machu Picchu, both near Cuzco and visited probably by nearly every traveller to that city. Yet they remained uncollected until 1943.

Undoubtedly one factor that has contributed largely towards these and other species remaining unknown up to now is their short growing season, since they die down for at least half the year and flower and vegetate only during the rainy season. As this season is not chosen by most sightseers and botanists owing to the unreliability of travel and the frequency with which bridges and roads are swept away by the rains in the wilder parts of the Andes, it is perhaps not surprising that many wild potatoes have remained undiscovered, though the two species from Cuzco would always be readily accessible. Later in the year when the rains are over and travel becomes relatively easy the haulms of wild potatoes are withered away, leaving no signs that their tubers are perennating under the ground, and hence unless their presence has been ascertained earlier in the year it is of course impossible to find them.

Yet although the reasons we have mentioned above for this lack of comprehensive wild potato collections do apply to a wide extent, a vast amount of botanical collecting has been done in the Andes and adjacent regions during all seasons of the year and by many different collectors.

Perhaps another and relatively more important factor that militates against the proper collection of wild potatoes has been the attitude of the collector himself. The 'pure' botanist in the past was extremely averse to collecting anything that might be a cultivated plant or an 'escape' from cultivation. Although not all wild potatoes bear a particularly close resemblance to the cultivated plant, some indeed differing so much as to be quite unidentifiable as anything remotely connected with a potato, a large proportion of the wild species definitely seem to bear some resemblance. Even the genuinely wild types, as distinct from the weed potatoes that are always to be found in the neighbourhood of dwellings and fields, those indeed that grow and flourish miles away from human habitation, were in the past regarded as possible escapes, and as such were very inadequately collected. Since on the whole wild potatoes, like their cultivated relatives, seem to favour rather open situations and a soil that is fairly rich in nitrogenous constituents they would naturally often be found to grow around dwellings. Furthermore, since, as has been demonstrated by one of us before (J.G.H. 1944), the tubers of wild potatoes are often collected for food by the Indians, it is quite possible that portions of skin or semi-rotten tubers may be discarded in the vicinity of the houses and will sprout and grow there as well as in their original habitat. In either of these two ways truly wild potatoes may therefore be found very often in the region of dwellings and have escaped collection by the travelling botanist.

Despite these several factors that have tended to prevent an adequate collection and survey of the wealth of material available, nearly 100 wild species had been described up to the twenties of the present century. With the large-scale potato collecting expeditions sent to Mexico and South America by the government of the U.S.S.R. in 1927–33 and the British Empire in 1938–9 much new and valuable information about wild potatoes was obtained. In addition, interest was stimulated in the potato amongst South American botanists so that new material is continually being discovered; some 170 wild species have now been described.

The genus *Solanum*, and especially subsection HYPERBASARTHRUM of section TUBERARIUM, to which the potatoes belong, may be compared in its complexity with such genera as *Rosa* where the distinguishing characters between the species are rather fine-drawn and the wealth of variation is enormous. It seems probable that the genus has recently passed or perhaps is still passing through a period of intensified species formation in which interspecific sterility barriers are not complete. Within the several groups or series into which the sub-section has been divided most species are more or less completely interfertile, and hybrids often are quite possible, though with decreasing fertility, between species belonging to different series. We still, however, know very little about the extent of natural species hybridization or the amount of gene interchange that goes on in the relatively intrafertile groups of species that have generally been classified as series. It is very possible that they might be considered as coenospecies.

Bukasov (1938, 1940) classes these groups of microspecies together as collective species (*species collectivae*). Thus *S. Commersonii* in the series COMMERSONIANA from Argentina includes in its wider sense (*sensu latiore*) according to Bukasov the microspecies *S. Commersonii* (*sensu stricto*), *S. Ohrondii*, *S. Henryi*, *S. sorianum*, *S. mercedense*, *S. mechonguense* and *S. laplaticum*. Also within this same series COMMERSONIANA there is another collective species *S. Parodii*, besides a number of other species whose relationships are not too clear. In the series LONGIPEDICELLATA from Mexico, CUNEOALATA from Bolivia and Argentina and ACAULIA from the Andes the collective species is one and the same thing as the series. The use of the concept of the collective species which may be found to be the same as the coenospecies when more information from experimental results is forthcoming is in some ways convenient in pointing out relationships, though it is not valid according to the International Rules of Nomenclature.

The new series MEGISTACROLOBA, proposed below, is completely unstudied in the living state, the diagnoses having been made from herbarium specimens only. This lack of living material applies unfortunately to probably at least half of the species of potatoes that have been described in the past. It makes a detailed study of their interrelationships necessarily limited and the taxonomy and phylogeny of the group very incomplete.

The next series to be dealt with in the present paper is TUBEROSA. This has been rather in the nature of a depository for species whose relationships and affinities are not very well known, as well as for those which quite definitely should be grouped here. *S. virgultorum*, *S. Weberbaueri* var. *poscoanum*, *S. mollepujroense* and the new varieties of *S. anomalocalyx* should certainly be placed in TUBEROSA but the position of *S. liriunianum* is not so clear.

S. xerophyllum should be placed in series CUNEOALATA.

The relationships of *S. capsicibaccatum* are still obscure. By virtue of its conical berries it should come within CONICIBACCATA. Its chromosome number, however, is $2n=24$, whilst that of the CONICIBACCATA species that have been studied in the living state is in every case $2n=48$. The leaf type also, differs considerably. It will therefore probably be better to leave it ungrouped until more is known of its growth and immediate relatives.

Before passing to the account of the detailed systematics of the material under review the authors wish to record their very grateful thanks to Dr Alice Koppel for making the Latin versions of the new species descriptions.

Series: MEGISTACROLOBA Cárdenas et Hawkes, **ser.nov.**

A seriebus aliis in subsectione HYPERBASARTHRO Bitter generis *Solani* L. foliolo terminali valde ampliato, foliolis lateralibus nonnumquam omnino reductis distinguitur. Foliola lateralia si praesentia generaliter latere basiscopico in rhachidem late decurrentia. A serie CUNEOALATA Hawkes habitu robustiore, foliolo terminali ampliato, ala *triangulari* a basi foliolorum laterâlium generaliter late decurrente facile distinguendum; foliola multum latiora, flores corolla rotatiore, majores.

Distinguished from the other series in subsection HYPERBASARTHRUM Bitter of the genus *Solanum* L. by the very enlarged terminal leaflet, sometimes with a total reduction of the lateral leaflets. The lateral leaflets when present are generally broadly decurrent on to the rhachis on the basiscopic side. Easily distinguished from series CUNEOALATA Hawkes by the more robust habit, enlarged terminal leaflet and generally wide *triangular* wing decurrent from the base of the lateral leaflets; the leaflets are much wider and the flowers larger, with more rotate corolla.

Plants low, probably all tuber-bearing, generally growing in a rosette but sometimes with decumbent branches, never attaining to any great size. Distinguished from the other HYPERBASARTHRUM series by the enlarged terminal leaflet and smaller basiscopically decurrent lateral leaflets. The leaf is generally imparipinnatisect rather than imparipinnate as in most other members of the HYPERBASARTHRUM. The leaves of series CUNEOALATA, although imparipinnatisect and with decurrent wings on the rhachis, differ completely from those of MEGISTACROLOBA, since in the latter series the leaflets are ovate, obovate, broadly ellipsoid, etc., with an enlarged terminal leaflet, whilst in the former the leaflets are lanceolate, linear-ovate, etc., and the terminal leaflet is not so greatly enlarged in comparison with the laterals.

The creation of the new series MEGISTACROLOBA brings together several little-known previously described species, namely: *S. megistacrolobum* Bitter, the type species, *S. alticola* Bitter, and *S. tilcarense* Hawkes. The following species to be described below are also grouped within series MEGISTACROLOBA: *S. raphanifolium* Cárdenas and Hawkes, *S. Hawkesii* Cárdenas, *S. decurrentilobum* Cárdenas and Hawkes, *S. toralapanum* Cárdenas and Hawkes, and *S. ellipsifolium* Cárdenas and Hawkes.

At least two trends can be observed within the series:

(1) The progressive narrowing of the wing decurrent on to the rhachis from the lateral leaflets or leaf lobes. The wing is least noticeable in *S. tilcarense*, *S. raphanifolium* and *S. megistacrolobum* whilst it is broadly triangular in *S. toralapanum*, *S. decurrentilobum* and *S. Hawkesii*.

(2) The other trend is towards the reduction of the lateral leaflets, resulting finally in species with a simple lamina. That the trend has taken this course rather than the reverse process of progressive complication from a simple leaf to a highly dissected one is largely a matter of conjecture. Nevertheless, when reviewing the totality of species within section TUBERARIUM the primitive non-tuberiferous species are nearly always provided with imparipinnate leaves. This is certainly so with those that are most closely related to the tuber-bearing species. The majority of the tuberiferous species also bear imparipinnate leaves whilst it is only in certain species that entire-leaved types are found, species which from other features one would not concede to be primitive or ancestral. Assuming, therefore, the possibility of an evolutionary trend towards simplification of the lamina in MEGISTACROLOBA it is worthy of note that this has also taken place in other related groups of species within HYPERBASARTHRUM, especially with the species grouped round

S. simplicifolium Bitter (*S. microdontum* Bitter, *S. bijugum* Bitter, *S. gigantophyllum* Bitter) and to a lesser degree in those species related to *S. Maglia* Schlechtd. (*S. medians* Bitter, *S. Molinae* Juz.).

In series MEGISTACROLOBA the best dissected leaves are found in *S. Hawkesii* Cárdenas (3–4 lateral jugae with a few interjected leaflets). *S. megistacrolobum*, *S. tilcarense*, *S. raphanifolium* and *S. toralapanum* are less well dissected and with a greater divergence in size between the terminal and lateral leaflets. In *S. toralapanum* var. *subintegrifolium* and *S. decurrentilobum* the laterals are still further reduced at the expense of the terminal leaflets and only 1–2 pairs are to be seen. With *S. alticola* Bitter var. *xanthotrichum* Hawkes occasional unijugate leaves are seen; in *S. ellipsifolium* small lateral lobes are quite uncommon. Finally, in *S. alticola* the lamina is entire, the lateral lobes having disappeared completely.

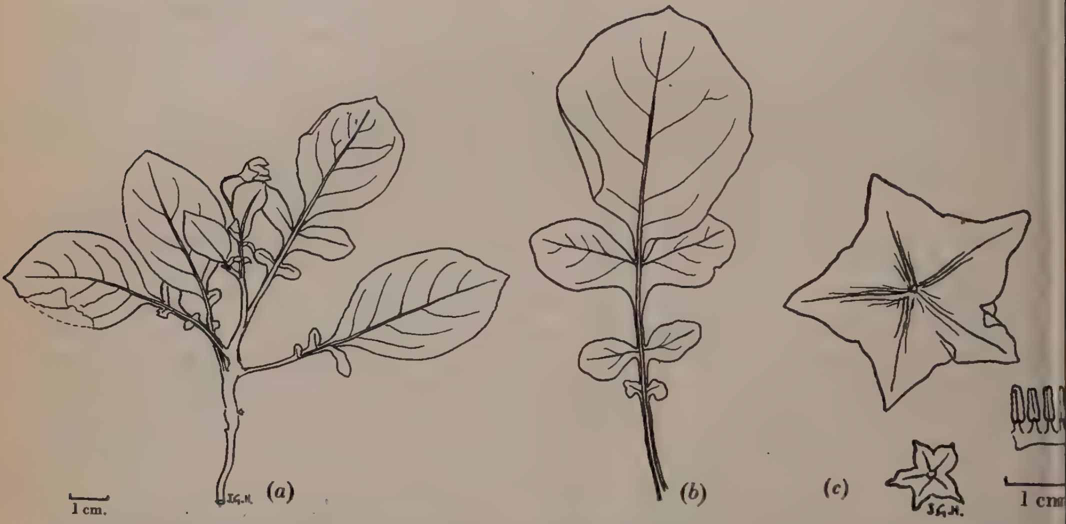


Fig. 1. *S. raphanifolium* Cárd. et Hawkes. (*a*) Young rosette plant. (*b*) Leaf. (*c*) Floral dissection.

SOLANUM RAPHANIFOLIUM Cárdenas et Hawkes, **sp.nov.**

Herbaceum, verisimiliter tuberiferum.

Planta habitu semi-rosulato vel secundum locum et aetatem ramis multis decumbentibus patula. *Caulis* in plantis rosulatis 3–10 cm. altus, pauci-ramosus; caulis in plantis patulis circa 3 cm. longus, crassus et erectus; ramos multos decumbentes usque ad 27 cm. longos emittens, glabrescens, pilis sparsissimis patulis provisus. *Folia* 5–13 cm. longa, 2–3 (–5)-juga (vel plantae basi uni-juga), 0–2-paribus foliolorum interjectorum parvorum sessilium per folium; foliola lateralia ovata vel obovata, sessilia; juga superiora 37 × 23, 28 × 17, 25 × 15 mm. etc., folii basin versus subito decrescentia; par supremum in rhachidem plusminusve decurrens, paria 2–5 minus manifeste decurrentia; foliolum terminale lateralibus multum majus, late obovatum vel obovatum vel ellipticum, apice leviter acuminatum, basi decurrens, 6·3 × 5·2, 5 × 3·5, 4 × 2·2, 3·5 × 2·5 cm. etc.; foliola omnia pilis breviusculis rigidis albis, supra crebris infra densis, obtecta. *Inflorescentia* 1–4-flora. *Pedunculus* 3–7 cm. longus, sicut folia pilis sparsis vel crebris provisus. *Pedicelli* 15–25 mm. longi, 4–9 mm. infra calycem articulati, pilis crebrissimis albis rigidis adpressis, glandulis quoque sparsis parvis stipitatis obtecti. *Calyx* circa 6 mm. longus lobis ovatis 3–5 mm. longis mucrone 1–2 mm. longo incluso, sicut pedicelli pubescens. *Corolla* violacea, rotato-stellata, 2·5–2·7 cm. diam.; lobo acumine non bene delimitato, basi 12 mm. lato × 7·5–11 mm. longo acumine triangulari 5 mm. longo incluso. *Antherae* 5·5–6 mm. longae × basi 1·75–2 mm. latae, apice ad 1·5 mm. attenuatae. *Stylus* crassus,

7·5–8 mm. longus, glaber vel inferius $\frac{1}{3}$ longitudinis nonnullis papillis minutis provisus. *Stigma* styli apice ampliata majus, globosum, circa 1 mm. diam. *Bacca* solitaria immatura globosa 5 mm. diam. visa est.—v.s.s.

PERU: Dept. Cuzco, prope Cuzco, Saxahuamán, Martio 1943. In collibus herbosis prope fortificationem Saxahuamán, a Dr M. Cárdenas et H. Gandarillas collectum. No. 3500 et 3501.

Affinitates: Seriei MEGISTACROLOBAE conjungendum propter foliolum terminale typice ampliatum et foliola lateralia, lobis satis similaria, in rhachidem plusminusve decurrentia. A *S. megistacrolobo Raphani* folio conformi, foliolo terminali late obovato, foliolis lateralibus minus distincte decurrentibus, corollae forma differt. A *S. decurrentilobo* folii corollaeque forma, characteribus etiam aliis omnino differt. Species distinctissima in serie.

The plant described under no. 3500 is spreading, with long decumbent branches and a slightly larger calyx; no. 3501 comprises the rosette plants with shorter stem and smaller calyx. The differences between the two numbers do not seem to us to warrant their separation into two varieties since the differences could easily be accounted for by slight differences of soil or exposure.

Should be placed within series MEGISTACROLOBA by virtue of the typically enlarged terminal leaflet and rather lobe-like laterals that are more or less decurrent on to the rhachis. The species differs from *S. megistacrolobum* in the resemblance of the leaf to that of *Raphanus*, broadly obovate terminal leaflet, less well-marked decurrency of the lateral leaflets and shape of the corolla. From *S. toralapanum* it differs chiefly in the leaf shape, lesser amount of pubescence and larger flowers with more triangular corolla lobes. From *S. decurrentilobum* it differs completely in the form of leaf and corolla as well as in other features. It is therefore a very distinct species in the series.

SOLANUM HAWKESII Cárdenas, **sp.nov.**

Herbaceum, tuberiferum.

Caulis subterraneus, crassus, 4 mm. diam., certe 30 cm. longus, an longior?, caulis superterraneus erectus vel ascendens, alis angustis $\frac{1}{2}$–1 mm. latis a foliorum basibus decurrentibus praeditus, glabrescens; internodiis satis brevibus, 1·5–4·5 cm. longis. *Folia* satis magna, infra 15–24 cm. longa, supra 13–18 cm. longa, (2–) 3–4-juga, foliolis interjectis nullis vel paucis sessilibus ovatis vel ovato-cordatis, 7 in foliis maxime dissectis sed generaliter 1–3, foliolis lateralibus ab apice basin versus celerrime decrescentibus, ovatis vel ovato-lanceolatis, subacuminatis, sessilibus, 1–2 (–3)-jugis distalibus latere basiscopico in rhachidem late decurrentibus, jugis minoribus non decurrentibus latere basiscopico vel acroscopico auriculatis; jugis distalibus lateralibus 1·5 × 2·5, 2·5 × 5, usque ad 3·5 × 7·5 cm.; foliolum terminale lateralibus majus, generaliter obovatum, nonnumquam obovato-ellipticum, apice sub-acuminatum, petiolulo 0·7–1·5 cm. longo, saepe jugo foliolorum interjectorum sessilium praedito; foliola omnia margine leviter denticulata pilis sparsis falcato-adpressis multi-cellularibus, superne pilis sparsioribus similaribus obtecta, subtus mesophyllo glabrescentia et venis venulisque pilis sparsis pauci-cellularibus praedita; folia pseudostipulacea ovata vel semi-lunata, generaliter 1 cm. longa, nonnumquam 2 cm. longa. *Inflorescentia* 7–11-flora. *Pedunculus* bifurcatus, 5–7 cm. longus infra, 2–3 cm. longus supra furcam, pilis sparsis adpressis pauci-cellularibus praeditus. *Pedicelli* 1·5–2·5 cm. longi, medio vel supra medium articulati, articulo 5–8 mm. infra calycem, pilis pauci-cellularibus vel uni-cellularibus et glandulis minutis breviter stipitatis satis dense obtecti. *Calyx* campanulatus, plusminusve 7 mm. longus, lobis ovatis, circa 2–3 mm. longis, in mucronem anguste triangularem 2 mm. longum subito angustatis; sicut pedicelli pilis glandulisque satis dense obtectus. *Corolla* coeruleo-purpurea (in specimine sicco) stella alba, 2·5–3 cm. diam., lobis membranis interpetalaribus longe conjunctis, 16 mm. latis et 7·5 mm. longis in parte libera, acumine 4 mm. longo incluso, extus acumina versus pilis satis densis pauci-cellularibus et glandulis minutis breviter stipitatis praeditis. *Filamenta* brevia, 1 mm. longa × basi 0·75 mm. lata. *Antherae* 6 mm. longae × basi 2 mm. latae, a basi apicem versus paulo angustatae, basi apiceque emarginatae. *Ovarium* profunde bisulcatum. *Stylus* 8·5 mm. longus, infra medium papillis densis minutis obtectus. *Stigma* styli apice paulo majus, ovoideo-conicum. *Bacca* non videbatur. v.s.s.

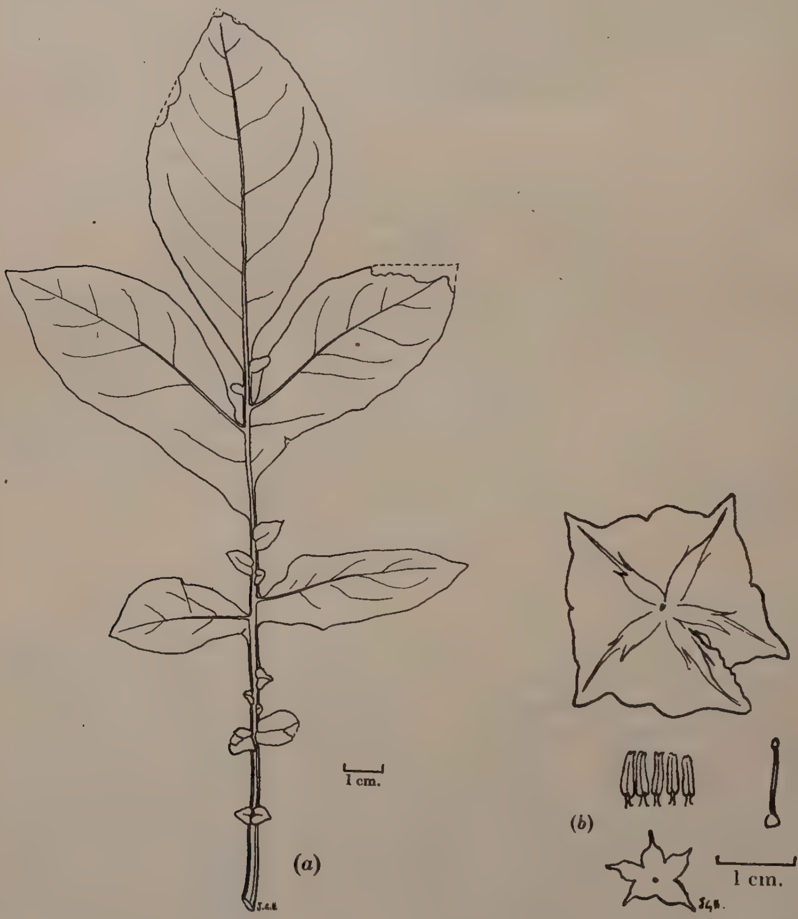


Fig. 2. *S. Hawkesii* Cárd. (*a*) Leaf. (*b*) Floral dissection.

Peru: Dept. Cuzco, Machu Picchu, altitudine plusminusve 2000 m. In margine silvae humidae a Dr Martín Cárdenas Martio 1943 collectum. No. 3506. Cl. Dr J. G. Hawkes dedicatum.

Affinitates: Seriei Megistacrolobae Cárdenas et Hawkes conjungendum propter foliola terminalia obovata ampliata et foliola lateralia superiora late decurrentia. A *S. megistacrolobo* Bitt. caule erecto, foliolis pinnatis (non pinnatilobatis), foliolis lateralibus superioribus latius decurrentibus, calycis acuminibus angustioribus et corollae lobis brevioribus differt; a *S. decurrentilobo* Cárdenas et Hawkes foliolis terminalibus minoribus, foliis minus pubescentibus plus dissectis, calycis lobis brevioribus et latioribus, corollae acuminibus longioribus et latioribus, stylo longiore et graciliore, stigmate minore differt.

Should be included in the series MEGISTACROLOBA Cárdenas and Hawkes by virtue of the enlarged obovate terminal leaflets and widely decurrent upper lateral leaflets. Differs from *S. megistacrolobum* Bitt. in the upright stem, the pinnate (not pinnatilobed) leaflets, the more widely decurrent upper lateral leaflets, narrower calyx acumens and shorter corolla lobes; from *S. decurrentilobum* Cárdenas and Hawkes it differs in the smaller terminal leaflets, less pubescent leaves, greater leaf dissection, shorter and broader calyx lobes, longer and wider corolla acumens, longer, thinner style and smaller stigma.

SOLANUM DECURRENTILOBUM Cárdenas et Hawkes, **sp.nov.**

Herbaceum, an tuberiferum? *Planta* habitu semi-rosulato patulo, caulibus nonnullis ascendentibus basi multi-ramosis. *Caulis* 2–4 mm. crassus usque ad 22 cm. altus, pilis crebris tenuibus albis patulis obtectus. *Folia* 10–23 cm. longa imparipinnatilobata, 0–3, generaliter 1–2-juga; lobus terminalis lateralibus multum major; folia parva ovalia simplicia usque ad 2·5–7·5 cm. longa × 1·3–2·5 cm. lata plantae basi occurrunt; lobus terminalis longus ovali-oblongus, apice leviter acuminatus, basi in rhachidem manifeste decurrens, 11·5 × 4, 11 × 3·5, 10 × 5, 8 × 3·2 cm. etc.; lobi laterales terminali minores, plusminusve ovales *ala latissime decurrente* usque ad lobi proximi latus acroscopicum pertinente, lobi ad 3 × 1·8 cm.; ala usque ad 4 cm. longa × apice 1·7 cm. lata; folium supra viride, infra pallidius, utrinque pilis satis crebris albis brevibus obtectum. *Inflorescentia*

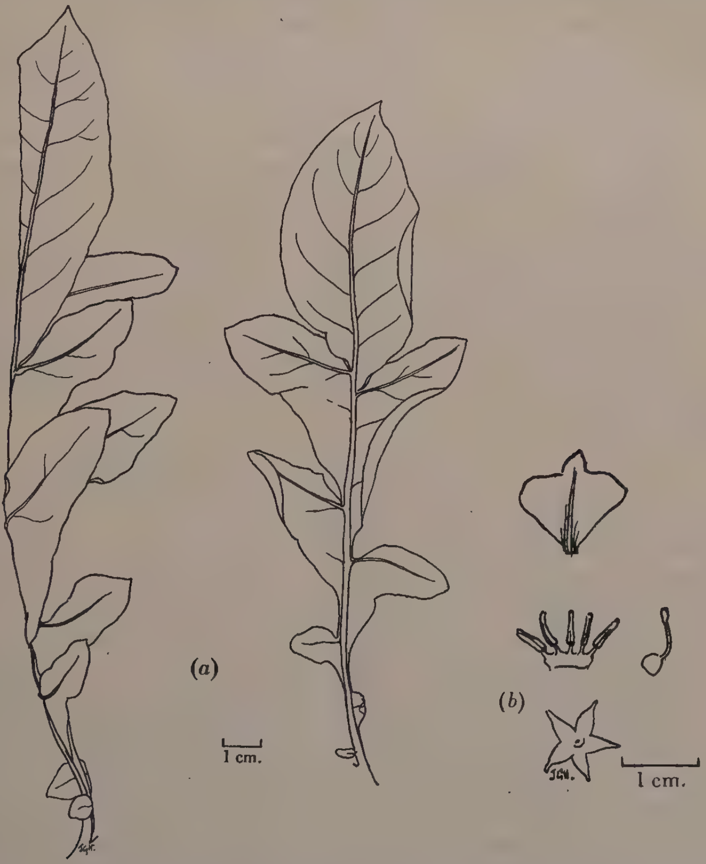


Fig. 3. *S. decurrentilobum* Cárd. et Hawkes. (*a*) Leaves. (*b*) Floral dissection. (Only a single petal drawn.)

(1)–3–6-flora. *Pedunculus* 5–8 cm. longus, circa $\frac{1}{3}$ longitudinis supra basin saepe folio simplici vel semi-unijugo provisus, sicut caulis pilis longis albis patulis obtectus. *Pedicelli* 1–2·5 cm. longi, 4–6 mm. infra calycem articulati, pilis albis patulis nonnulli-cellularibus atque glandulis parvis breviter stipitatis immixtis obtecti. *Calyx* campanulatus, 6–9 mm. longus, lobis ovato-lanceolatis acuminatis 4·5–7 mm. longis acumine non bene delimitato 1·5–4 mm. longo incluso; calyx extra pilis densis albis et glandulis minutis obtectus; calyx in floribus minoribus (Cárdenas No. 3502) lobis 10 × 7 mm. *Corolla* atro-violacea plusminusve 2·5 cm. diam., lobis in floribus melius evolutis basi 16 mm. latis × 10 mm. longis acumine 3 mm. longo incluso. *Filamenta* plusminusve 1 mm. longa. *Antherae* 5–5·5 mm. longae × basi 2 mm. latae, apicem versus ad 1·5 mm. attenuatae. *Stylus* crassus, 6–8 mm. longus, $\frac{1}{3}$–$\frac{1}{2}$ longitudinis supra basin papillis dispersis minutis sub microscopio conspicuis obtectus. *Stigma* magnum plusminusve globosum emarginatum (in Cárdenas no. 3502), 1–1·25 mm. diam. *Bacca* immatura globosa vel leviter conica, circa 8 mm. diam.—v.s.s.

Bolivia: (1) Dept. Cochabamba, prov. Arani prope Tiraque, Hacienda Toralapa, 3700 m. in agris humiferis ubi *Solanum andigenum* cultum, Feb. 1944 a Dr M. Cárdenas collectum. No. 3503. (2) Dept. Cochabamba, prov. Ayopaya prope Morochata, Hacienda Piusilla, 3000 m. in terra humifera a Dr M. Cárdenas Feb. 1944 collectum. No. 3502.

Affinitates: *S. megistacrolobo* et *S. toralapano* folii typo et habitu affine. A *S. megistacrolobo* folii lobis latius decurrentibus, indumento densiore, calyce majore, corollae lobis latioribus etc. differt; a *S. toralapano*, etiam folii latius decurrentibus, indumento longiore et patuliore, calyce majore, corollae lobis latioribus etc. differt.

In Cárdenas no. 3502 the calyx corresponds with the larger, the corolla with the smaller and the stigma with the larger dimensions given in the above description.

Related to *S. megistacrolobum* and *S. toralapanum* in the leaf type and habit of growth. Differs from *S. megistacrolobum* in the more widely decurrent lateral lobes of the leaf, denser pilosity, larger calyx, wider corolla lobes etc.; from *S. toralapanum* it differs also in the more widely decurrent lateral leaf lobes, longer and more spreading pilosity, larger calyx, broader corolla lobes, etc.

SOLANUM TORALAPANUM Cárdenas et Hawkes, **sp.nov.**

Herbaceum, an tuberiferum? Habitu rosulato complanato, circa 30 cm. diam. *Caulis* brevissimus, basi ramosus ramis nonnullis prostratis 6–7 cm. longis. *Folia* impari-pinnata vel imparipinnatisecta, 14–17 cm. longa, 1–4-juga; foliola lateralia ovata, obtusa, sessilia *alis manifestissime decurrentibus triangularibus*; foliola distalia usque ad 4 × 2·3 cm., generaliter circa 3 × 1·8 cm.; 1–2 foliola interjecta minuta orbiculata sessilia interdum praesentia; foliolum terminale ovato-rotundum vel anguste obovatum vel ellipticum, basi in rhachidem sensim attenuatum, apice obtusum et mucronatum, 1·5 × 3·5, 3·3 × 6, 4·5 × 7 cm. etc.; foliola omnia laete viridia supra, satis palliora et argentea infra, supra pilis satis crebris, infra et in margine satis densis, brevibus hispidis obtecta. *Inflorescentia* pauci- (1–4)-flora. *Pedunculus* in statu florente 1·5 cm. longus, in statu fructescente 3 cm. longus hispido-pilosus sicut folia, pilis etiam brevioribus minoribus provisus. *Pedicelli* 2·8 cm. longi (an interdum longiores?), circa 4 mm. infra calycis basin articulati, pilosi sicut pedunculus. *Calyx* circa 5 mm. longus, sepalorum pars libera 3–4 mm. longa × basi 2·5 mm. lata, mucrone 1 mm. longo incluso, extra pilis satis longis rigidis praeditus. *Corolla* rotata, atro-violacea, diam. 1·75 cm. (an infloribus melius evolutis longior?), petali pars libera basi 10 mm. lata, 7 mm. longa. *Filamenta* 1 mm. longa. *Antherae* 4·5 × basi 2 mm. latae, apicem versus ad 1 mm. angustatae. *Stylus* satis crassus, glaber 6 mm. longus. *Stigma* fere globosum 1 × 1·25 mm. longum, a styli apice satis bene delimitatum. *Baccae* solum immaturae videbantur, globosae.—v.s.s.

Bolivia: Dept. Cochabamba, prope Tiraque, Hacienda Toralapa, 3700 m. In terra humifera ubi *Solanum andigenum* cultum. A Dr Martín Cárdenas Febr. 1944 collectum. No. 3504.

Affinitates: *S. megistacrolobo* affine, sed alis distinctius triangularibus a foliorum lateralium lateralibus basiscopicis decurrentibus, plantae totius pubescentia densa albida hispido-pilosa, calyce corollaque majore etc., differt. *S. megistacrolobo* forma rosula, folii typo (etiamsi alis multum distinctius in rhachidem decurrentibus), calyce antheris stylo conformibus, ita recte in serie Megistacroloba includendum.

This species is related to *S. megistacrolobum* but differs in the more strongly triangular wings decurrent from the basiscopic sides of the lateral leaflets, the dense whitish hispido-pilose pubescence over the whole plant, larger calyx and corolla, etc. It agrees with *S. megistacrolobum* (thus justifying its inclusion in series Megistacroloba) in the following characters: plant growing in a rosette, with similar leaf type though with much more strongly marked decurrent wings on the rhachis, calyx anthers and style of similar type.

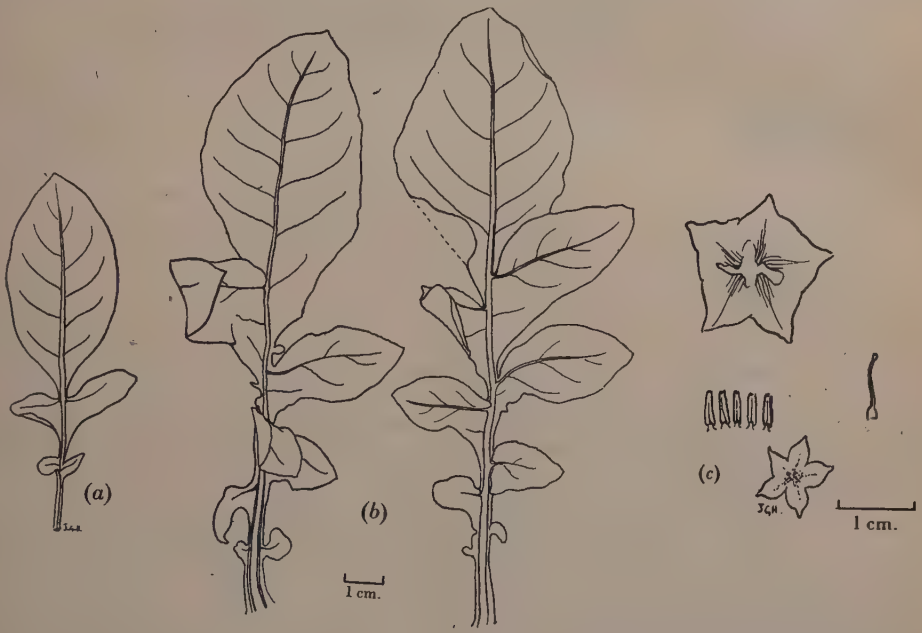


Fig. 4. *S. toralapanum* Cárd. et Hawkes. (*a*) Young leaf. (*b*) Older leaves. (*c*) Floral dissection.

Solanum toralapanum var. subintegrifolium Cárdenas et Hawkes, **var. nov.**

Herbaceum, an tuberiferum? Habitu rosulato complanato. *Caulis* supra terram omnino absens, infra terram 6 cm. longus an longior? *Folia* integra vel folioli terminalis valde ampliati basi 1–2 paribus loborum parvorum sessilium praedita; foliolum terminale longo-ovatum vel longo-ellipticum, 12 × 6·4, 14 × 6·2, 7 × 3·4, 6 × 2·5 cm. etc., apice rotundatum vel leviter acutum, basi in rhachidem anguste alatam sensim attenuatum; lobi laterales vel absentes vel parvi, sessiles, ad 7 mm. longi, latere basiscopico manifeste decurrentes, vel in casu uno 25 × 14 mm., ovati; facies sicut in *S. toralapano* pilis crebris vel densis albidis hispido-pilosis obtecta. *Inflorescentia* pauci-flora. *Pedunculus* 4·5 cm. longus. *Pedicelli* plusminusve 2·3 cm. longi, 5–7 mm. infra calycem articulati, sicut pedunculus pilis densis albis brevibus provisi. *Calyx* typo conformis, mucronibus leviter longioribus. *Corolla* atro-violacea, diam. 2 cm.; lobus basi 13 mm. latus × 8 mm. longus. *Antherae* et *filamenta* typo similaria. *Stylus* crassus, glaber, 7 mm. longus. *Stigma* globosum, vix 1 mm. diam., styli apice non bene delimitatum. *Baccae* non videbantur.—v.s.s.

Bolivia: Dept. Cochabamba, prope Tiraque, Hacienda Toralapa, 3700 m. alt. in agris humiferis ubi *S. andigenum* cultum Febr. 1944 a Dr M. Cárdenas collectum. No. 3505 p.pte.

Affinitates: Typo foliolis terminalibus plus ampliatis, foliolis lateralibus in lobos parvos reductis differt. Florum characteres non multum differunt.

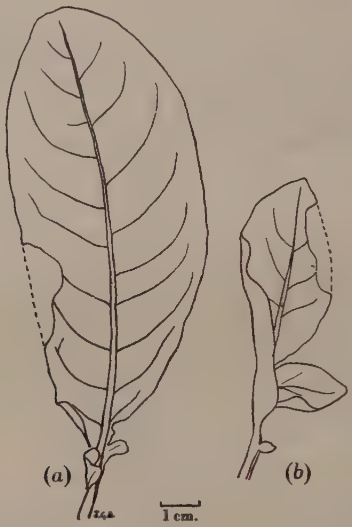


Fig. 5. *S. toralapanum* var. *subintegrifolium* Card. et Hawkes. Leaves: (*a*) older, (*b*) younger.

Differs from the type in the much greater enlargement of the terminal leaflets and the reduction of the laterals to small lobes. The floral characteristics do not differ very considerably.

SOLANUM ELLIPSIFOLIUM Cárdenas et Hawkes, **sp.nov.**

Herbaceum, tuberiferum; tuberibus globosis 1·5 cm. diam., habitu rosulato complanato. *Caulis* supra terram vel non evolutus vel usque ad 1·5 cm. longus, infra terram 3–7 cm. longus vel verisimiliter etiam longior. *Folia* integra vel *rarissimo* 1–2 foliolis lateralibus parvis sessilibus instructa; lamina late elliptica, 7·5 × 5·5, 6·2 × 3·5 cm. etc., folia basalia fere orbiculata, apice mucronata, basi obtusa, nonnumquam 1–2 lobis parvis sessilibus praedita, 3–10 mm. longis; folia supra pilis brevibus frequentibus rigidis, infra in venis venulisque solum pilis infrequentioribus obtecta; petiolus brevis, 0·5–1 cm. longus. *Inflorescentia* pauci (1)-flora. *Pedunculus* 1–3 cm. longus, bractea parva elliptica 1·3–2 cm. longa praedita. *Pedicelli* 22–25 mm. longi, 5–6 mm. infra calycem articulati, sicut folia pilosi. *Calyx* 7–8 mm. longus lobis ovatis acuminatis basi 2·5 mm. latis, circa 1 mm. longis; calyx extra pilis albis rigidis obtectus. *Corolla* rotata, atro-violacea, circa 20 mm. diam., lobis rotundatis basi circa 10 mm. latis × 7 mm. longis acumine non bene delimitato incluso. *Filamenta* brevia, 0·75 mm. longa et lata. *Antherae* 5 mm. longae × basi 1·25 mm. latae, apicem versus attenuatae. *Stylus* 8 mm. longus, crassus, supra ampliatus, in stigma capitatum magnum emarginatum, circa 1 mm. diam., 0·75 mm. altum, subito ampliatus; stylus glabrescens, papillis mamillatis minutissimis sub microscopio vix conspicuis provisus. *Baccae* non videbantur.—v.s.s.

Bolivia: Dept. Cochabamba, prope Tiraque, Hacienda Toralapa, in terra humifera prope agros ubi *Solanum andigenum* cultum; altitudine 3700 m. Feb. 1944 a Dr M. Cárdenas collectum. No. 3505 p.pte.

Affinitates: A speciebus in serie Megistacroloba jugis lateralibus omnino reductis differt. *S. alticolae* Bitter quod est species alia seriei eiusdem lamina omnino simplici

provisa, proximum; ab eo foliis latius ellipticis (in *S. alticola* lanceolatis) basi apiceque subitius attenuatis, calyce majore, corolla rotata, antheris majoribus, stylo longiore praecipue differt.

Differs from the other species in series Megistacroloba by the almost complete reduction of the lateral jugae. It is probably closely related to *S. alticola*, the other species in this series where the lamina is completely simple; it differs from that species however chiefly in the more broadly elliptic leaves (lanceolate in *S. alticola*) which narrow more abruptly at base and apex, larger calyx, rotate corolla, larger anthers and longer style.

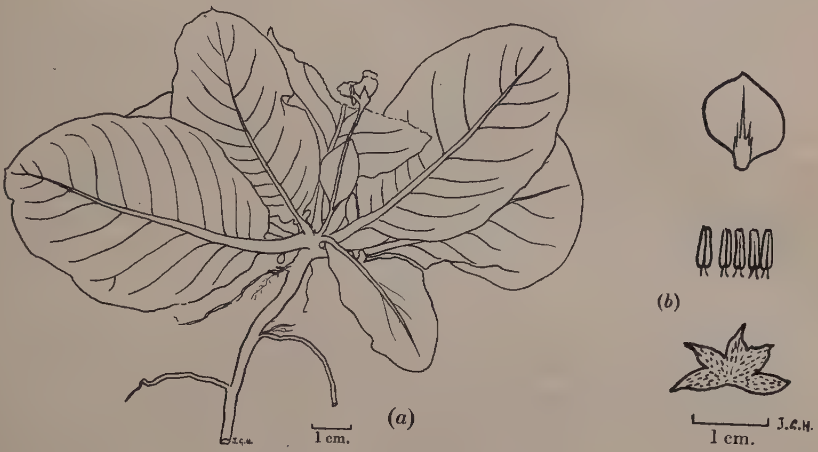


Fig. 6. *S. ellipsifolium* Cárd. et Hawkes. (*a*) Whole plant. (*b*) Floral dissection. (Only a single petal drawn.)

With this should also probably be included certain plants collected by E. K. Balls, W. B. Gourlay and J. G. Hawkes from the Quebrada de Colomi near potato districts of the same altitudes, 15 March 1939. Balls no. 6241, E.P.C. 119. The plants did not possess flowers and hence were not placed with certainty by Hawkes (1944) except that their affinities with *S. boliviense* and *S. alticola* were surmised.

Series: TUBEROSA Rydb.

SOLANUM WEBERBAUERI var. POSCOANUM Cárdenas et Hawkes, **var.nov.**

Solum pars superior florens visa. *Caulis* pilis sparsissimis, lineis decurrentibus vix prominentibus praeditus. *Folia* usque ad 17 cm. longa, interrupte imparipinnata, 3(–4)-juga, foliolis interjectis paucis, 2–4 per folium, foliolis a basi apicem versus celerrime ampliatis, minimis ovatis 0·5–1·3 cm. longis, supremis ovato-lanceolatis 6·0 × 2·6 cm., omnibus breviter (usque ad 3 mm.) petiolulatis, latere basiscopico in rhachidem late decurrentibus, rhachide ipsa anguste alata; foliolum terminale lateralibus majus 6 × 4 usque ad 10 × 5 cm. longum, ovato-lanceolatum, apice attenuatum, basi in rhachidem alatam sensim attenuatum; petiolulus ipse circa 8 mm. longus nonnumquam foliolo interjecto parvo ovato praeditus; foliola utrinque pilis pauci-cellularibus, subtus venorum lineis sparse obtecta; folia pseudostipulacea plerumque praesentia, parva. *Inflorescentia* 9-flora. *Pedunculus* brevis (an longior deinde?) folium reductum parvum gerens. *Pedicelli* 12–18 mm. longi, solum circa 2½–3 mm. infra calycem articulati, sicut pedunculus pilis satis crebris albis patulis multicellularibus obtecti. *Calyx* patulus, magnus, bi-trilabiatus, (2 + 3 vel 2 + 2 + 1) usque ad 1·5 cm. diam., lobis basi 2 mm. latis × 7–8 mm. longis acumine 3–4 mm. longo incluso; calyx omnino pilis densis patulis albis multi-cellularibus commixtis pilis glandulisque minoribus uni-cellularibus obtectus. *Corolla* verisimiliter violacea (laete

violacea vel albida in specimine sicco) circa 2 cm. diam., lobis 9 mm. latis × 7–8 mm. longis in parte libera acumine 4 mm. longo incluso, extus praecipue apicem versus pilis brevibus multi-cellularibus et glandulis sparsis pauci-cellularibus praedita. *Filamenta* brevia circa 1 mm. longa. *Antherae* 6 × basi 2 mm., apice angustatae, 1 mm. latae. *Stylus* 8 mm. longus, glaber. *Stigma* globosum, styli apice paulo majus, leviter bifidum.—v.s.s.

PERU: Dept. Arequipa, Islai, Lomas de Posco, 600–900 m. 'Areno-pedregoso'. A Dr C. Vargas 1 Aug. 1940 collectum. No. 2019.

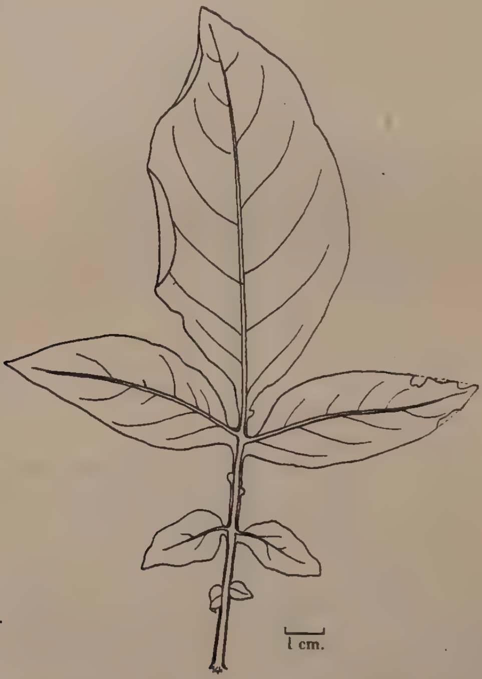


Fig. 7. *S. Weberbaueri* Bitt. var. *poscoanum* Cárd. et Hawkes. Leaf.

Affinitates: Propter folii formam et magnitudinem similarem et florum characteres *S. Weberbaueri* conjungendum; tamen foliolis interjectis frequentioribus, folii faciei inferioris pubescentia sparsiore, pedicellis altius articulatis, calyce paulo majore, corolla minore, filamentis brevioribus, stigmate paulo majore differt. Var. *poscoanum* a *S. neoweberbaueri* cui *S. Weberbaueri* proximum, foliolis angustioribus minoribus, terminalibus majoribus ad lateralia, foliolis interjectis minoribus, pilis in pedunculis et pedicellis longioribus, pedicellis brevioribus, corolla minore in facie externa glabra sine pilis glandulatis atris, antheris paulo majoribus stylo *omnino glabro* differt.

Should be placed with *S. Weberbaueri* on account of the similarity of leaf shape and size, and floral characteristics: it differs however in the more frequent interjected leaflets, the sparser pubescence of the under surface of the leaf, the higher pedicel articulation, slightly larger calyx, smaller corolla, shorter filaments and slightly larger stigma. From *S. neoweberbaueri* to which *S. Weberbaueri* is closely related, var. *poscoanum* differs in the smaller narrower leaflets, the terminal larger in proportion to the laterals, smaller interjected leaflets, longer hairs on peduncle and pedicels, shorter pedicels, smaller corolla with no dark glandular hairs on the external surface, slightly larger anthers and completely *glabrous style*.

SOLANUM VIRGULTORUM (Bitter) Cárdenas et Hawkes, **comb.nov.**

S. boliviense Dun., subsp. *virgultorum* Bitt. in *Fedde Rep.* XII, 1913, pp. 153–4 = *S. virgultorum* (Bitt.) Cárdenas et Hawkes comb.nov.

S. virgultorum was described by Bitter as a subspecies of *S. boliviense* Dun., though he stated in his description that it 'differs strikingly in its habit from the *S. boliviense* type known up to now', adding further 'but a more detailed knowledge of the type and the subspecies in question is necessary, mainly as regards the shape and form of the berries'.

In our opinion, not only is *S. virgultorum* specifically distinct from *S. boliviense* but it is not at all closely related to that species, differing in the habit, the 1–2 jugate leaves (never more than unijugate in *S. boliviense*), rather different floral parts, longer style and larger stigma. It should probably be grouped with *S. microdontum* Bitt., *S. bijugum* Bitt. and *S. simplicifolium* Bitt.

The Kew specimen of *S. virgultorum*, although presumably used by Bitter as a basis for his description, differs in several characteristics, chief among them being the shorter stem with shorter internodes, only 1–1·5 cm. (2–3 cm. in Bitter's description), and lateral leaflets *not* decurrent on to the rhachis; the pubescence of the leaves is more dense than in the original description whilst the stigma seems more elongated than Bitter's term 'subglobose' would indicate.

S. virgultorum differs from *S. bijugum* (to which it bears many affinities) in the shorter stem, leaves generally uni- occasionally bijugate but lower jugae when present much smaller than in *S. bijugum*, leaflets smaller and more acuminate, petiolule shorter, inflorescence fewer-flowered, calyx smaller, corolla not white but probably violet (slightly pigmented on one petal of the Kew specimen), style not glabrous, stigma larger etc.

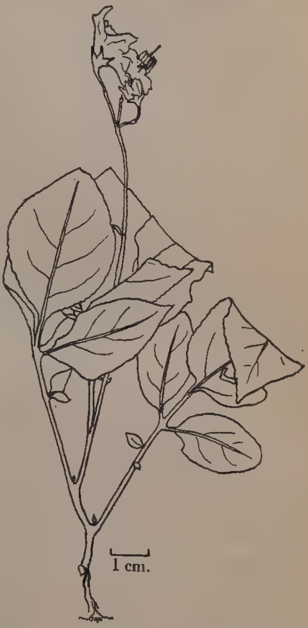


Fig. 8. *S. virgultorum* (Bitt.) Cárd. et Hawkes. Flowering stem. (Traced from specimen in Herb. Hort. Kew.)

Compared with *S. microdontum* it differs in the smaller size of the plant, number and smaller size of leaflet jugae, upper laterals not decurrent on to the rhachis, fewer-flowered inflorescence, calyx without long attenuated lobes, corolla probably not white, style with more papillae, and longer stigma; it agrees in the covering of many-celled acute hairs on the upper leaf surface.

SOLANUM MOLLEPUJROENSE Cárdenas et Hawkes, **sp.nov.**

Herbaceum, an tuberiferum? *Caulis* semi-erectus, multiramosus, 24–27 cm. longus; internodia inferiora 8–15 mm. longa. *Folia* atro-viridia, 11–16 cm. longa, 4–5-juga; foliola lateralia elliptico-lanceolata apicem versus sensim acuminata, paulo rotundata vel saepe basi latus acroscopicum versus late auriculata; foliola suprema 35–50 × 12–15 mm.; foliolum terminale ovato-lanceolatum, satis distincte acuminatum (5–6 × 1·5–2·5 cm.); rhachis et petioluli ala 1 mm. lata pubescenti provisa; foliola interjecta, 2–3 paria, quorum 1 vel 2 parva (4–5 × 2–2·5 mm.) nonnumquam ad rhachidis partem distalem infra folium terminale inserta; foliola omnia utrinque et in marginibus pilis sparsis pauci-cellularibus obtecta; folia pseudostipulacea brevia, 5 mm. longa, basi tamen lata; foliolorum et foliorum pseudostipulatorum margines subdentatae. *Inflorescentia* 3–8-flora. *Pedunculi* bifurcati, infra furcam 2·5–3 cm. longi. *Pedicelli* 9–12 mm. longi, in vel supra medium articulati, articulo obsolescenti; pedunculi pedicellique pilis albis brevibus densiter

obtecti. *Calyx* 4–5 mm. longus; lobi 3–5 mm. longi vel irregulariter partiti vel bi-labiati (2+2+1), mucronibus 1–1·5 mm. longis tenuissimis. *Corolla* coeruleo-violacea, 25–30 mm. diam., lobis 2–3 mm. longis, 11 mm. latis. *Filamenta* 1 mm. longa. *Antherae* conicae, 4 mm. longae. *Stylus* crassus, 8 mm. longus, per totam longitudinem papillosus. *Stigma* styli suprema parte crassius, globosum, bi-lobulatum.—v.s.s.

BOLIVIA: Dept. Cochabamba, prov. Tarata, Mollepujro (degrediens ad Rio Caine), a Dr M. Cárdenas Martio 1944 collectum. No. 3510.

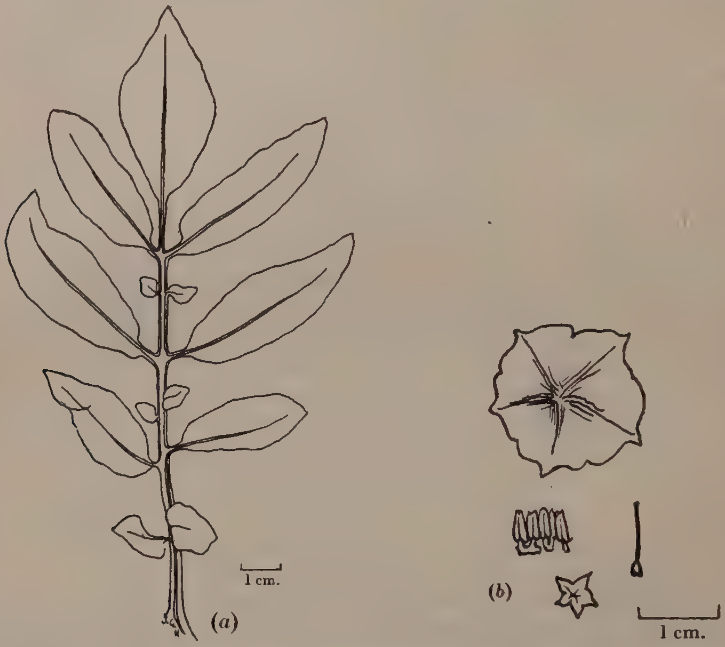


Fig. 9. *S. mollepujroense* Cárd. et Hawkes. (*a*) Leaf. (*b*) Floral dissection.

Affinitates: A *S. anomalocalyce* Hawkes differt; habitu inculto vel semi-inculto, calyce paulo anomali affine; habitu minore, caule plus ramoso, foliis foliolisque longioribus et angustioribus, floribus infrequentioribus, calyce corollaque breviore differt. *S. pachytricho* Hawkes foliolorum lanceolatorum forma leviter simile, sed caulibus longioribus foliis plus dissectis, foliolis lateralibus longioribus et latioribus, foliolis interjectis semi-basiscopicis absentibus, pedunculis longioribus, calyce breviore, corolla majore, filamentis longioribus ab eo differt. *S. mollepujroensis* characteres praecipui: foliola satis glabra et longe lanceolata, flores pauci.

Differs from *S. anomalocalyx* Hawkes to which it is related by its weed or semi-wild occurrence and somewhat irregular calyx on account of the following characters: shorter habit, more branched stem, longer and narrower leaves and leaflets, fewer flowers, shorter calyx and corolla. By the shape of its lanceolate leaflets it reminds one somewhat of *S. pachytrichum* Hawkes, but differs from it by the longer stems, more dissected leaves, longer and wider lateral leaflets, lack of semi-basiscopic interjected leaflets, longer peduncles, shorter calyx, larger corolla, longer filaments. The chief distinguishing characters of this species are the almost glabrous, long lanceolate leaflets and few flowers.

SOLANUM ANOMALOCALYX Hawkes var. LLALLAGUANIANUM Cárdenas et Hawkes, **var.nov.** Herbaceum, tuberiferum. *Caulis* erectus 30–35 cm. longus, in parte inferiore 3–4 mm. diam., alis 1 mm. latis crispis praeditus. *Folia* 4-juga, 16–20 cm. longa, foliolorum interjectorum deltoideo-ovatorum 4–7 paribus, aliis in rhachide alata, aliis basiscopicis praesentibus; foliola lateralia 5–8·5 × 2–4 cm., ovata vel elliptico-lanceolata apice acuminata basi acutiuscula, longe petiolulata, 0·5–1 cm. longa; petioluli nonnumquam ala angusta decurrenti praediti; foliolum terminale ovatum apice valde acuminatum, basi acutum, 3·5–10 × 1–5·5 cm. petiolulo incluso; foliola omnia utrinque et margine pilis sparsis albis provisa; foliola tenuissima et membranacea; folia pseudostipulata orbiculata, 5–7 × 10 mm. in foliorum axillis praesentia. *Inflorescentia* 12–15-flora. *Pedunculus* 2 cm. longus, pilis laxissimis sparsis obtectus. *Pedicelli* 8–20 mm. longi, in statu florente leviter pubescentes, in ⅓ partis superioris vel interdum juxta medium articulati. *Calyx* 6 mm. longus, campanulatus, lobis irregulariter (1 + 1 + 1 + 2) partitis; lobi subito in mucronem filiformem 1–1½ mm. longum angustati, pilis multi-cellularibus obtecti. *Corolla* 18–20 mm. diam. coeruleo-purpurea; acumina 4 mm. lata, 1½ mm. longa, in marginibus pilis albis densiter obtecta. *Antherae* tuba cylindrica, 6 mm. longa, laete flavidae. *Filamenta* in parte libera 1 mm. longa. *Ovarium* globosum. *Stylus* 8 mm. longus, pubescens vel in parte inferiore papillosus. *Stigma* styli apice multum crassius, fulvum, manifeste bilobatum.—v.s.s.

Habitat. BOLIVIA: Dept. Cochabamba, prov. Tarata. (1) Llallaguani, prope Anzaldo, circa 2900 m., a H. Gandarillas Jan. 1944 collectum. Cárdenas No. 3508. (2) prope Angostura, 2550 m., a Dr M. Cárdenas Febr. 1944 collectum. No. 3518.

Affinitates: Cum *S. anomalocalyce* Hawkes jungendum propter habitum et calycem irregulariter partitum; ab eo foliis majoribus minus dissectis (16–20 cm. longis), foliolis interjectis paucis, foliis tenuibus membranaceis, pedunculis pedicellisque brevioribus, calycis mucronibus brevioribus, corolla minore, stigmate majore bilobulato differt.

Should be placed with *S. anomalocalyx* Hawkes on account of the general habit and irregular calyx division. Differs from the type species in the larger less dissected leaves (16–20 cm. long), fewer interjected leaflets, thin membranaceous leaves, shorter peduncles and pedicels, shorter calyx mucrons, smaller corolla and larger and bilobulate stigma.

SOLANUM ANOMALOCALYX var. BRACHYSTYLA Cárdenas et Hawkes, **var.nov.**

Herbaceum, tuberiferum. *Caulis* erectus 28–45 cm. altus, ala angusta leviter crispa pubescente provisus. *Folia* 3–4-juga, 8–12 cm. longa, 3–4 paribus foliolorum interjectorum ovatorum vel orbiculatorum; foliola lateralia 2–4 × 1–2 cm., elliptica, in facie superiore atrius viridia; foliolum terminale 2·5–5 × 1·5–3 cm., ovatum ellipticum, apice sensim acuminatum; foliola lateralia interdum semi-decurrentia; foliola omnia utrinque et in marginibus pilis laxis sparsis obtecta; folia pseudostipulacea praesentia. *Inflorescentia* 8–10-flora. *Pedunculus* infra furcam 3–7 cm. longus. *Pedicelli* 6–12 mm. longi, 4–8 mm. longi infra articulum, pubescentes. *Calyx* 4–5 mm. longus, irregulariter (1 + 1 + 1 + 2) partitus, lobis marginibus 1 mm. latis membranaceis translucidis, pubescens, subito mucronatus, mucrone minus quam 1 mm. longo. *Corolla* coeruleo-purpurea, radio 12–15 mm.; acumen utrinque pilis densis albis obtectum. *Filamenta* tenuissima, 1 mm. longa. *Antherae* 6 mm. longae luteo-flavidae. *Stylus* 8 mm. longus, tenuis, glaber, antheras solum 1 mm. excedentes. *Stigma* crassum, leviter bilobulatum. *Bacca* globoso-ovata, 11 mm. diam.—v.s.s. in herb. Cárdenas.

BOLIVIA: Dept. Cochabamba. (1) Prov. Cercado, La Maica 2550 m., a Dr M. Cárdenas Febr. 1944 collectum. No. 3519. (2) Prov. Arani, supra Arani, 2700 m., a Dr M. Cárdenas Martio 1944 collectum. No. 3520.

Affinitates: Cum *S. anomalocalyce* Hawkes propter habitum et calycis morphologiam generalem jungendum. A var. *llallaguaniano* plantae habitu brevi, foliis minoribus, calyce minus bilabiato, stylo brevissimo differt.

Should be referred to *S. anomalocalyx* Hawkes on account of the general morphology of calyx and habit. Differs from var. *llallaguanianum* in the shorter length of the plant, smaller leaves, less bilabiate calyx and the short style in comparison with the length of the stamen column.

SOLANUM ANOMALOCALYX Hawkes var. MURALIS Cárdenas et Hawkes, **var.nov.**

Herbaceum, tuberiferum. *Caulis* 13–15 cm. longus, in plantis minoribus xerophilosis flexuosus et nodosus; ala angustissima praesens. *Folia* 5–9 cm. longa, 3 (–4)-juga; foliola lateralia lanceolata, apice acuta, basi acuta vel satis rotundata (2–4 cm. × 8–15 mm.); foliolum terminale oblongo-lanceolatum apice acutissimum (2·5–5 × 1·5–2 cm.); foliola interjecta (3–4-paria) parva, semper in rhachide; foliola omnia utrinque et in marginibus pilis sparsis paucis obtecta; folia pseudostipulacea lata praesentia. *Inflorescentia* 4–7-flora. *Pedunculi* infra furcam 1–2 cm. longi, omnino glabri. *Pedicelli* 8–14 mm. longi supra medium articulati, pubescentes. *Calyx* 4–5 mm. longus, campanulatus; lobi nonnumquam regulariter saepe irregulariter partiti (1 + 1 + 1 + 2), leviter acuminati vel subito in mucronem attenuati, pubescentes et lateraliter in marginem angustam membranaceam transientes. *Corolla* coeruleo-violacea, 15–18 cm. diam.; acumina 2 mm. longa × 3 mm. lata, densiter pubescentia. *Filamenta* 1 mm. longa. *Antherae* 5 mm. longae. *Stylus* antheras 4 mm. superans, tenuis, satis glaber. *Stigma* stylo paulo crassius, claviforme.—v.s.s.

BOLIVIA: Dept. Cochabamba, prov. Cercado, La Maica, 2560 m. in muris siccis et arenosis occurrens, a Dr M. Cárdenas Martio 1944 collectum. No. 3507.

Affinitates: *Solani anomalocalycis* varietas minima et gracillima, tamen a typo et a var. *brachystyla* supra descripta foliis (3[–4]-jugis) minus dissectis, foliolis interjectis minoribus, corolla minore, habitu distinctissime xerophiloso (quod ad muros lutosos siccos crescit) differt.

This is the smallest and most slender variety of *S. anomalocalyx*, but differs from it and the var. *brachystyla* described above, by the less dissected leaves (3–[4–]-jugate), smaller interjected leaflets, smaller corolla, and its marked xerophilous character, since it grows on dry clay walls.

Note. The original species *S. anomalocalyx* Hawkes, belonging to the semi-spontaneous or weed potato group, seems to possess a great amount of variation according to its wide geographical distribution in or near cultivated ground. It is to be expected, therefore, that more subspecies, varieties and forms will be found in the central temperate valleys of South America.

SOLANUM LIRIUNIANUM Cárdenas et Hawkes, **sp.nov.**

Herbaceum, tuberiferum. *Caulis* erectus, a nodo ad nodum flexuosus, circa 20 cm. altus, alis mediocriter latis rectis a foliorum basibus decurrentibus provisus, pilis satis crebris patulis multi-cellularibus albidis obtectus. *Folia* 4–5-juga, usque ad 19 × 11 cm., foliolis interjectis numerosis sessilibus ovato-cordatis 2–13 mm. longis, circa 3–16 per folium; foliola lateralia satis remota inter se, ovata vel ovato-lanceolata vel lanceolata, apice acuminata, basi obliqua sessilia vel breviter (1–3 mm.) petiolulata, 6 × 2·3, 5 × 2, 3 × 1·4 cm. etc.; foliolum terminale lateralibus non majus, obovato-lanceolatum vel lanceolatum 5 × 2·2, 4·7 × 1·7 cm. etc.; foliola omnia supra pilis crebris albis multi-cellularibus, infra frequentissimis brevioribus instructa; folia juniora densissime pubescentia; foliola pseudostipulacea auriculata in foliolorum principalium axillis 15 × 10, 9 × 4 mm. etc. *Inflorescentia* terminalis, multi (–14)-flora. *Pedunculus* erectus, bi-furcatus, 7·5 cm. (an longior?) infra, 1·5–6 cm. supra furcam, pilis inaequilongis multi-cellularibus albis densissime obtectus. *Pedicelli* 2–3·5 cm. longi, circa $\frac{1}{3}$ longitudinis infra calycem articulati, itaque circa 7–11 cm. longi supra articulum *ampliatum*; pedicellus articulum versus sensim ampliatus, supra articulum tenuior et denuo calycis basin versus sensim ampliatus, sicut pedunculus pilis crebris inaequilongis articulo densissime obtectus. *Calyx* circa 7 mm. longus × 7 mm. diam., atro-purpureus, lobis ovatis in acumen 2 mm. longum angustatum; lobis acumine incluso 5 mm. longis; calyx omnis pilis frequentissimis albis multi-cellularibus accumbentibus obtectus. *Corolla* rotata, atro-purpurea, stella viridiuscula bene delimitata, circa 3 cm. diam., lobis complanatis basi 1·5 cm. latis, 7–9 mm.

longis acumine 3–5 mm. longo triangulari incluso. *Filamenta* plusminusve 2 mm. longa glabra. *Antherae* 6 mm. longae × 2 mm. latae, elliptico-oblongae, basi apiceque emarginatae. *Stylus* circa 10 mm. longus, apicem versus sensim ampliatus, inferius $\frac{1}{3}$ longitudinis papillis minutis crebris obtectum. *Stigma* styli apice non crassius, capitatum, emarginatum. *Baccae* non videbantur.—v.s.s.

BOLIVIA: Dept. Cochabamba, 18 km. N.W. a Cochabamba, prope Liriuni, 3000 m. altitudine, 5 Febr. 1943. In virgultis humidisparvis ad colles crescens. A Hugh Cutler No. 7690 collectum. 'Petals deep purple or blue-violet' sec. collectorem.

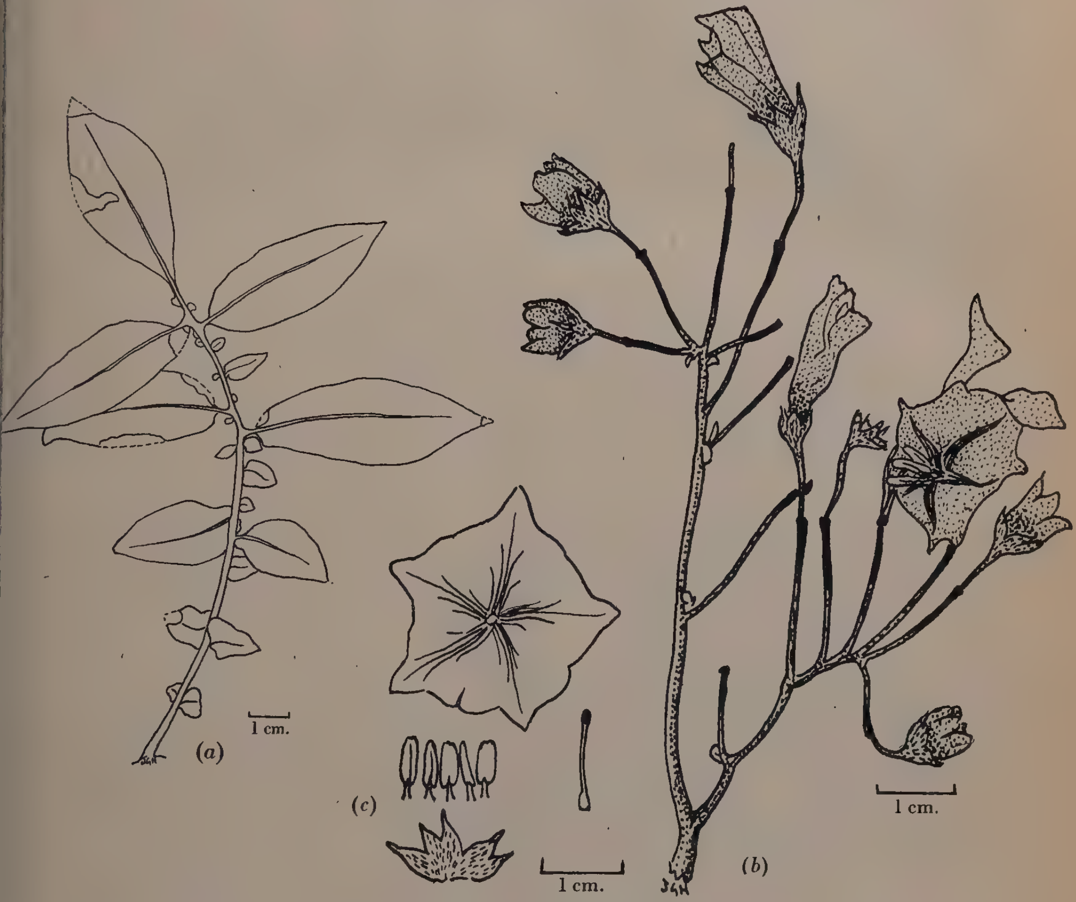


Fig. 10. *S. liriunianum* Cárd. et Hawkes. (*a*) Leaf. (*b*) Inflorescence. (*c*) Floral dissection.

Affinitates: *S. liriunianum* a *Solanorum* speciebus aliis incultis foliolis satis angustis, pubescentia albida, pedicellis longis rectis articulo incrassato, corolla atroviolacea, stylo longo apice incrassato, differt.

S. liriunianum is distinguished from the other wild potato species by the rather narrow leaflets, whitish pubescence, long straight pedicels with swollen articulation, deep violet corolla and long style swollen at the apex.

By the numerous long pedicels this species might be supposed to bear some relationship to series LONGIPEDICELLATA Buk. known up to now only from Central Mexico. The leaves, also, are not unlike those of *S. longipedicellatum* Bitter. It differs, however, in the completely different corolla and longer calyx lobes as well as in the denser and longer pubescence of the peduncle, pedicels and calyx. The chromosome number of the LONGIPEDICELLATA

series is $2n=48$ but unfortunately no living material of *S. liriunianum* is available; in consequence no counts of the chromosome number of this new species can be made until it has been re-collected in the form of tubers or seeds.

Solanum capsicibaccatum Cárdenas

(Emended transcription from the original diagnosis which appeared in *Revista de Agricultura, Cochabamba-Bolivia,* 1944, II, 35–36.)

Herbaceum, tuberiferum 20–40 cm. altum. Stolones valde tenues et breves; tuberibus magnis usque ad 15 mm. diam. rotundatis vel conico-elongatis (numquam complanatis) cuticula flavida et carne aquosa. *Caulis* gracilis flexuosus 1–1·5 mm. crassus paulo ramosus, superne striatus viridis, teres nigratus in parte inferiore, glaber. Internodia in partibus medianis caulis 1·5–2·5 cm. longa. *Folia* valde membranacea laxa, petiolis 2–3 cm. longis, pilosis. Lamina 5–8 cm. longa numquam simplex, vel foliolo laterali uno minuto vel plerumque 1–2-jugo, vel foliolis primi paris alternantibus vel oppositis; foliolum terminale 4·5–7 × 2·5 cm. ovatum, apice subacutum, basi vel attenuatum vel auriculatum; foliola lateralia 1–5 × 1–3 mm. usque ad 4 × 1·2 cm.; foliola omnia pallido-viridia marginibus leviter pilosis. Folia pseudostipulacea 2–3, minuta (8 × 3 mm.) caulis apicem versus sensim majora (15 × 5 mm.) vel lanceolata vel semi-lunata acuta. *Inflorescentia* 2–4-flora, primo pedunculis in axilla folii ultimi 2 cm. longis glabris. *Pedicelli* 6–11 mm. longi fere medio articulati. *Calyx* late campanulatus valde pilosus 3 mm. diam. lobis apice acuminatis 2 mm. longis. *Corolla* albido-lutea 15–20 mm. diam. lobis lanceolatis 5–6 × 2–3 mm. *Antherae* 3–4 mm. longae plusminusve ellipsoideo-lanceolatae. *Stylus* 8–9 mm. longus gracilis stamina superans. *Stigma* 0·5 mm. diam. apice sulcatum. *Baccae* conicae 2–3 cm. × 5–6 mm. virides purpurea maculatae, fructus juniores *Capsici frutescentis* revocantes.

BOLIVIA: Dept. Cochabamba, prov. Tarata.—Half-way down between Huaira Pata and Molle Ppujru, valley of the Rio Caine, 2800 m. In stony dry places in the shade of *Schinus molle* trees. H. Gandarillas 1942, No. 60.—Cárdenas and Gandarillas, April 1944 with tubers and berries, same locality. No. 3600 type in Imperial Agricultural Bureaux Potato Herbarium, Cambridge.

This species is probably related to *S. circaeifolium* Bitt. which came from the province of Larecaja (near Sorata), dept. La Paz, at 2650 m., but it differs in the dissection of its more definitely pinnate leaves and by the absence of hairs on the corolla lobes.

Tubers of this species were brought to England by Dr M. Cárdenas and grown at the Imperial Bureaux Potato Research Station, Cambridge, under the number E.P.C. 1701. Root tip samples were obtained and sectioned in 1945 in order to ascertain the chromosome number. This was found to be $2n=24$.

Series: CUNEOALATA Hawkes

SOLANUM XEROPHYLLUM Hawkes, **nom.nov.**

Solanum microphyllum Hawkes in *Bull. Imp. Bur. Pl. Breed. and Genet.* June 1944, p. 36 (*non S. microphyllum* Dun. in *Hist. Solan.* p. 187) et *S. pinnatifidum* Cárdenas in *Rev. Agric., Cochabamba,* July 1944, p. 33. =*S. xerophyllum* Hawkes, nomen novum.

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An account of some abnormal plants of Salvia Verbenaca L. and S. pratensis L.; together with a physiological interpretation of the phenomena observed in terms of growth hormone concepts. By D. A. Coult.

(With Plate 4 and 9 Text-figures)

[Read 9 May 1946]

Introductory and historical

In the summer of 1939, material of *Salvia Verbenaca* L. was collected from a Hertfordshire garden, and through the kindness of Sir Edward J. Salisbury, three abnormal shoots came into the hands of the author. Since that time, further abnormal material has been collected, mostly of *S. pratensis* L., from two gardens in Liverpool. The following account, whilst reporting in greater detail certain features of variation in this genus alluded to elsewhere (see Clos, 1879; Penzig, 1922; and Steinheil, 1835), aims also at discussing these features with reference to the theory of 'binding whorls' due to Schoute (1936, 1938), and also in relation to their possible bearing on the state of affairs which obtains at the normal Labiate shoot-apex. The variations encountered include the occurrence of two-topped and bifid leaves and bracts, abnormal distortion of the stem, and modification of the normal decussate system of phyllotaxis so characteristic of the Labiates in general.

Steinheil (1835) described a shoot of *S. Verbenaca* in which a 'two-topped' leaf was succeeded by an apparently normal leaf. He assumed that the latter was the fusion product of the paired leaves succeeding the former, in which fusion of the leaf pair was less complete. But he also described a plant of *Scabiosa atropurpurea*, in which one leaf of a pair was itself two-topped, and subtended a branch with leaves in whorls of three. Clos (1879) supported him in his suggestion that here was an instance of a leaf which was two-topped through splitting of the initial leaf rudiment. This is an explanation of the origin of two-topped leaves that Schoute (1936, p. 675), with some justification, has opposed; but discussion of his remarks will be more appropriate at a later stage.

Burkill & Wright (1899) described a genus of the Labiatae (viz. *Icomum* Hua) in which the narrow leaves were borne upon the stem in a close spiral succession; a similar feature is also seen in the bracts on the spikes of some species of the closely allied genus *Aeolanthus*. The same feature may be observed in the flowering spikes of the *Heteranthera* section of the genus *Scutellaria*.

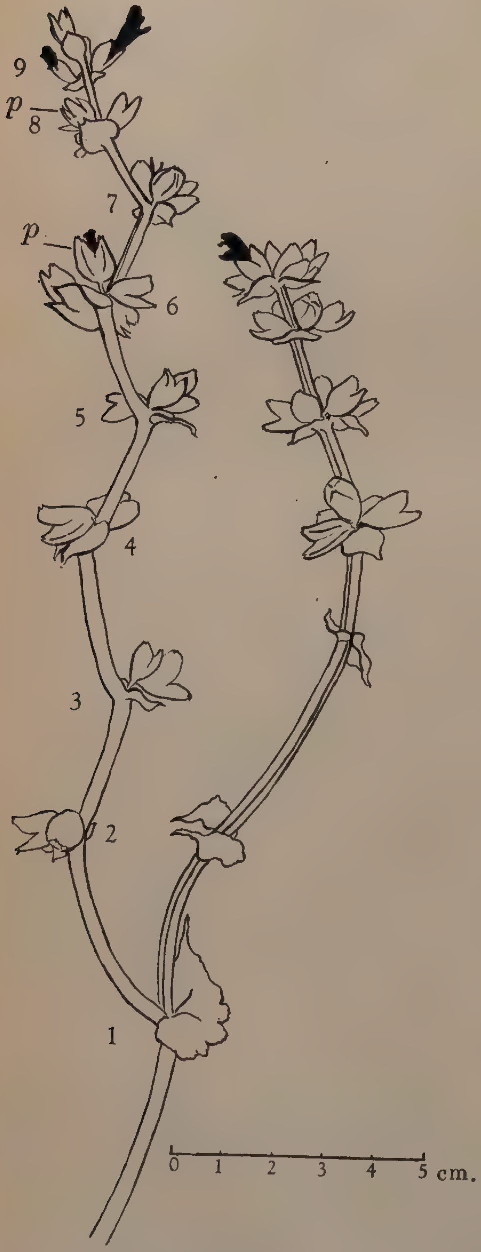
It will be recalled that these two species of *Salvia*, *S. pratensis* and *S. Verbenaca*, are very closely related. *S. pratensis* differs from the latter essentially only in its generally larger size, in its less deeply cut, but rather longer leaves, and in its larger and more showy corolla. Bentham, in his *Labiatarum Genera et Species* (1833), includes both in the section *Plethiospace*.

Shoot A (*Salvia Verbenaca*)

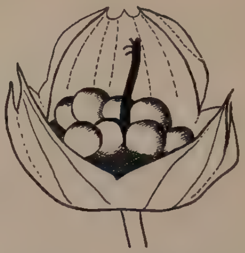
Description of material

As will be seen from Text-fig. 1, the abnormal spike showed erratic zigzag growth, and subtended basally a normal lateral spike bearing six decussate pairs of bracts. The four distal nodes of the normal spike showed the verticillasters typical of the genus. Below these, the two basal nodes subtended only flowerless peduncles, or undeveloped flowers, with the usual bracteoles.

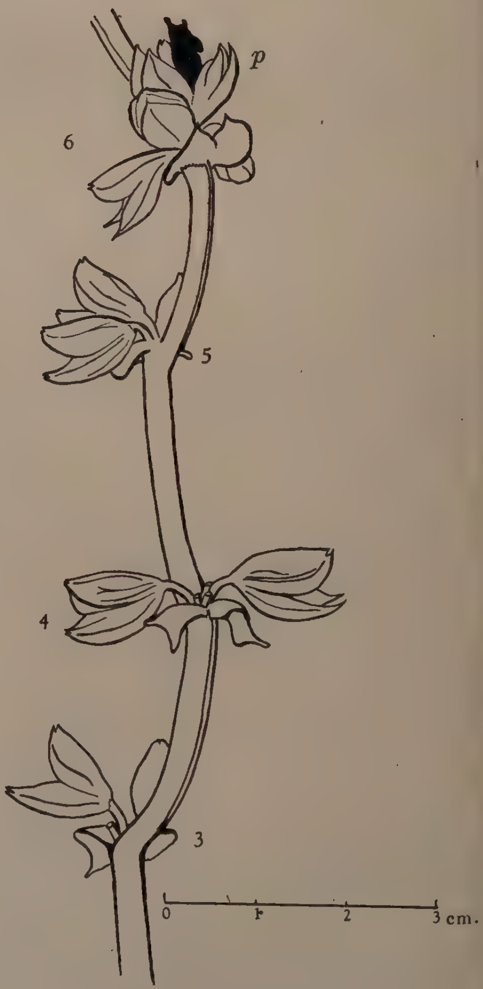
Both above and below the insertion of this normal shoot, the main abnormal shoot was flattened in a plane at right angles to that containing both shoots. It showed ten nodes and a terminal bud; these will be referred to in acropetal succession. No further material was available below the first, basal node, where a single normal leafy bract subtended the normal lateral described above. At the second node the bract subtended a normal cyme of three flowers, and was bifid at the tip, showing an incision of 1·5 mm. The bract at the third node was short and rather wide, but otherwise normal; it also subtended a cyme of three flowers. At the fourth node there were two bracts, free to their point of insertion, but together occupying a position alternating with the bracts above and below. Only two



Text-fig. 1. Shoot A (*Salvia Verbenaca*).
p, peloric flower.



Text-fig. 3. Peloric flower
from node 6, shoot A.



Text-fig. 2. Enlarged portion
of shoot A.

flowers were present, but there were three flowerless peduncles, as shown in Text-fig. 2. The bracts at the fifth, seventh and ninth nodes were normal, and subtended quite normal cymes. At the sixth node there was a bifid bract with a somewhat wider incision than that of the bract at the second node. It subtended four flowers, of which one was peloric. The peloric flower (Text-fig. 3) showed eight nutlets instead of the usual four, and had a multifid style. The eighth node showed a similar arrangement with one peloric, but only two normal flowers. The tenth node showed a little-developed but apparently normal bract which subtended only one flower. The terminal bud was sectioned and showed two further young bracts, but the material was insufficiently well preserved to offer critical information as to the current behaviour of the shoot apex.

Discussion of shoot A

It is at once apparent that there has been some profound disturbance of the growing point of the affected stem, and this is reflected not only morphologically, but also in the structure of the adult parts of the shoot.

Salvia normally shows the typical four-angled stem of the Labiatae, with regions of prominent vasculation at the angles, and of less prominent vasculation along the sides of the stem. Following the older anatomists, one may refer to the strands of these respective regions as cauline and common bundles. The cauline bundles, which make up the vasculation at the angles of the stem, continuously preserve their regional identity; they are reinforced below successive nodes by entrant leaf-traces, the so-called common bundles. Anatomical investigation of the flattened stem showed its essentially 'bipolar' nature. There were apparently only two cauline strands and two regions with common bundles; bracts were inserted alternately on one side or the other of the wide faces of the flattened stem, and contributed common bundles to its vasculation. Anatomically, therefore, it appears that virtually only half of a stem is represented. For reasons unknown, the procambial sector that would have developed into two cauline strands, together with a region of common bundles between them, has not developed. One can thus regard this flattened stem as a product of meristem which has given rise to two cauline strands, one region of common bundles associated with the insertion of normal bracts, and one such region which is dual in nature, reflecting as it does the insertion of bifid or paired bracts. In view of the fact that the other two aberrant shoots (B and C), available from the same source, showed a modified 1/3 phyllotaxis, it would be equally if not more reasonable to think of the present example as due to the modification of a stem with this phyllotactic system; the omission of a cauline strand and the fusion of two regions of common bundles could have resulted in the present state of affairs. Presumably this is conditioned by changes at the shoot-apex which influence the induction of leaf rudiments, although this does not wholly explain the absence of one or more of the prominent strands. Support is given to the belief that these are not entirely of leaf origin, and there is some justification for the retention of their description as cauline strands.

Schoute (1936) supposed that the occurrence of leaves in whorls in many families, including the Labiatae, was due to a so-called 'binding factor', operating from an early stage in the development of the leaf rudiments. If the linking of leaf rudiments by such a 'factor' is involved in shoot A, it is evident that it is regularly periodical in its operation, in the sense that the growing point alternately produces two leaf rudiments which are more or less connate, and one leaf rudiment which is never affected by the operation of the 'factor'. The 'factor' is thus either discontinuous in its application and effects, or, as appears to be more likely, it is functionally continuous, and unilateral or sectorial in operation with respect to the shoot apex.

Shoot A appears to correspond in some measure with shoots of *Salvia Verbenaca* and *S. janthina* described by Penzig (1922). There is, however, an important difference in that in these shoots there was apparently a regular alternation on a zigzag stem of constantly two-topped leaves. The 'binding factor' here does not seem to have operated unilaterally, but has apparently linked each successive pair of leaf rudiments as they have been induced. There is no evidence in this instance whether the stems were flattened and bipolar as in shoot A, or triangular as in shoots B and C. But from the descriptions of these shoots B and C which follow, it will be realized that they have almost achieved the regular alternation of bifid leaves, described by Penzig for his specimens. With regard to the abnormality of individual flowers in shoot A it will have been noticed that peloric flowers occurred only where there were bifid bracts. Such peloria could be explained as due to fusion, through congenital overcrowding of the flower bud rudiments in the axils of these bifid bracts; they could also be interpreted as arising through the operation of a similar process to that which results in the association of leaves. It was noticeable that there was no abnormality in the lateral flowers of those cymes showing peloria; presumably these lateral flowers had sufficient space from their earliest stages for normal development; alternatively they were induced at a relatively later stage and thus escaped the influence of the 'binding factor'.

SHOOTS B AND C (*SALVIA VERBENACA*)

Description of material

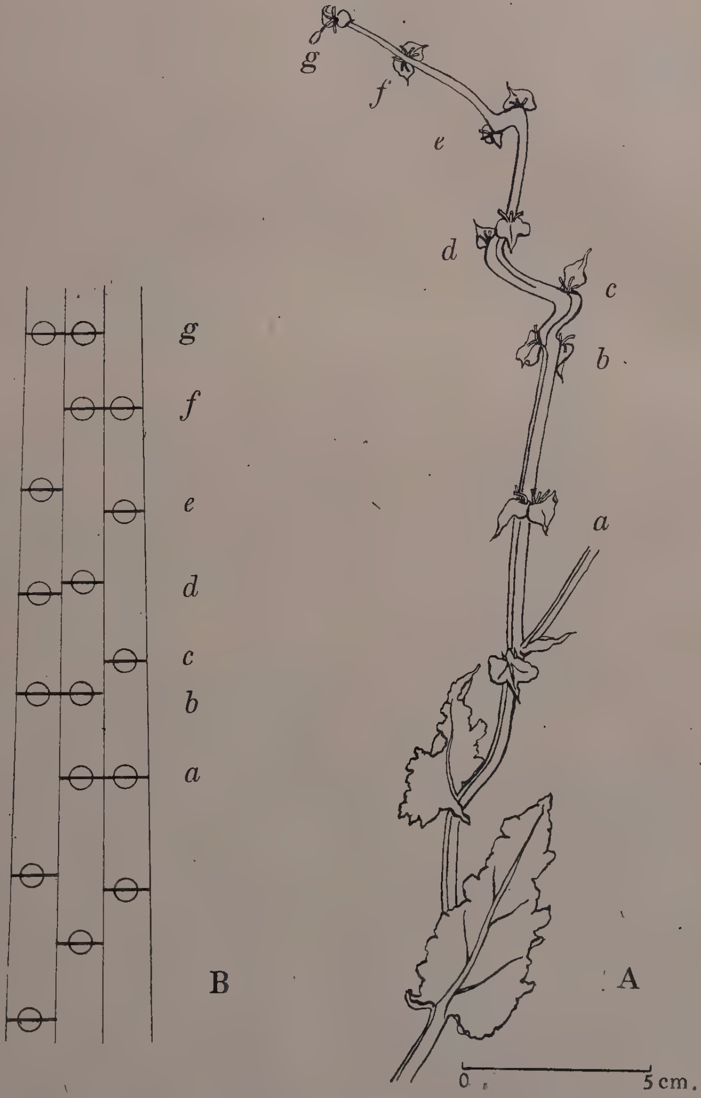
Shoots B and C of the Hertfordshire material afford evidence of the occasional uneven operation of the 'binding factor', in both instances operating on shoots with a theoretical leaf divergence of 120°, and with markedly triangular stems. Reference to the accompanying sketches (Text-figs. 4, 5) will help to clarify the position.

In shoot B (Text-fig. 4), the three lowest leaves were alternate, but they were otherwise normal and were fully vegetative. The fourth leaf was closely associated with or 'bound' to the third, and subtended a normal lateral which may for present purposes be disregarded. In succession to these leaves, as flowering had further imposed itself upon the shoot, were borne respectively the two pairs of bracts shown at nodes *a* and *b*, a single bract at node *c*, and four succeeding pairs of bracts, more or less closely associated, at nodes *d*, *e*, *f* and *g*. Distortion of the stem, which was maximal at node *c* bearing a single bract, seemed to increase wherever there appeared to be a difference in level between two bracts at a node. The extreme instance of this was at node *e*, though it could also be seen by comparing node *a* (where two bracts were inserted at practically the same level) with node *b*, where there was a small difference in level and some distortion.

On the other hand, in shoot C (Text-fig. 5), in which four of the available nodes showed two-topped leaves (two being bracts and two wholly vegetative), the same pattern for distortion was not so closely adhered to; bending of the axis in this case was associated mostly with nodes *c*, *e* and *f* (see figure). The leaf at *c* was two-topped and transitional. At *e* and *f* the bracts were respectively two-topped and single. A little bending occurred at *a* where there was a single vegetative leaf, but there was little distortion at *b*, with a two-topped vegetative leaf, at *d* with a single bract, or at *g* with a bifid bract.

For convenience, a phyllotactic plan of leaf insertions in shoots B and C is shown with each sketch (Text-fig. 4B and 5B respectively). In shoot B the association of leaves is apparently irregular and the production of regularly alternating pairs of bracts just fails to be achieved. It is possible that the shoots reported by Penzig may have conformed to some such similar pattern. This shoot is evidently most closely related in type with shoot A, where, however, the stem is two-faced, and flattened rather than triangular in section. This feature reflects the failure of shoot A to produce a main vascular strand (or cauline bundle) between the two associated ranks of bracts; its failure so to do does not support the contention of certain authors (see, for example, Esau, 1943) that such strands are entirely of leaf origin.

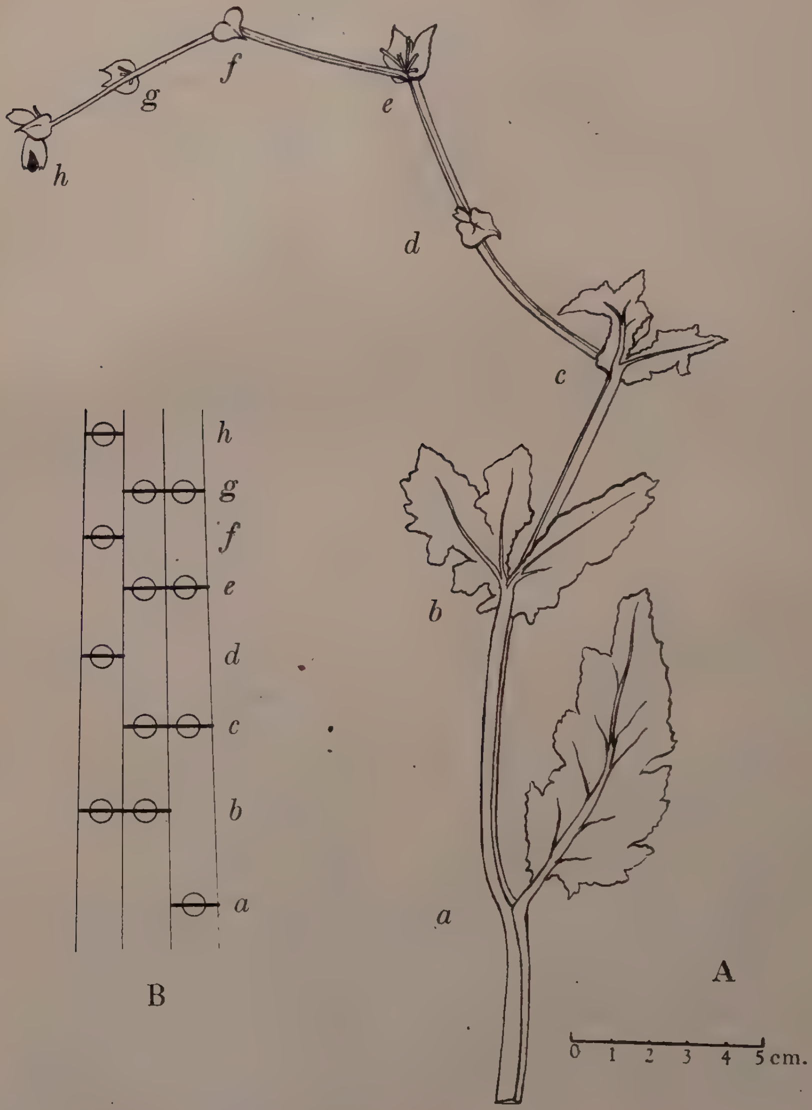
The remaining observations in this communication relate to material of *Salvia pratensis*, collected in the summer of 1944 from two gardens in Liverpool, which serves to implement the observations made above, and affords evidence of two methods by which the operation of a 'binding factor' of the type visualized could bring about a change in phyllotaxis, from a normal decussate shoot to the type with trimerous whorls that may occasionally be seen both in this genus and in other members of the family.



Text-fig. 4. A. Shoot B (*Salvia Verbenaca*). B. Theoretical phyllotactic plan. (Only vertical distances to scale.)

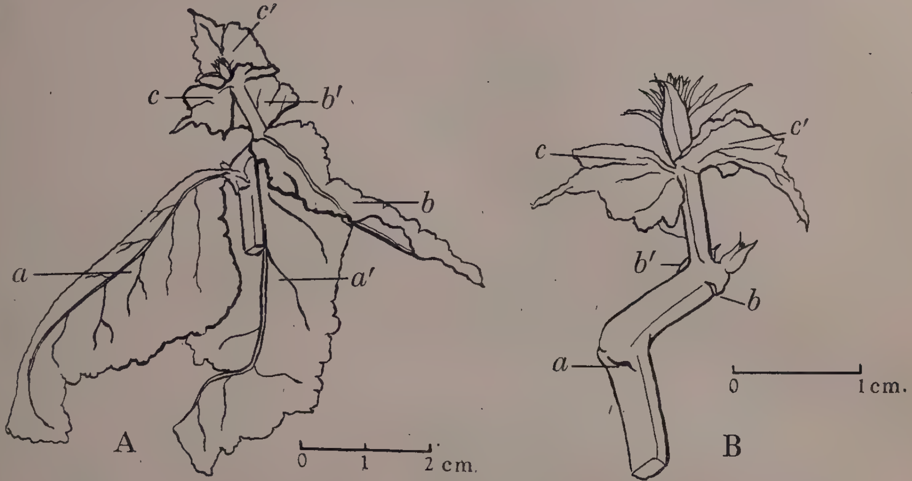
SHOOTS D AND E (*SALVIA PRATENSIS*)

The inflorescence of shoot D was normal, except for a lateral branch in which one bract of a pair was 'bound' to the two bract members beneath it. In consequence of this, its partner, which subtended a typical partial inflorescence, remained solitary, and distortion of the axis had occurred at the insertion of this solitary bract. Though there was spatial separation between the lower paired bracts and the bract from the upper pair which had thus become associated with them, it was notable that there was no distortion at this point, a pertinent reminder of the variability in operation of the factor which brings about displacement of the axis.



Text-fig. 5. A. Shoot C (*Salvia Verbenaca*). B. Phyllotactic plan.

Another younger shoot (E) of *S. pratensis* showed variation of this type carried to a further stage; it occurred in the vegetative part of the shoot just below the very young condensed inflorescence. Axial distortion first occurred (see Text-figs. 6 A, 6 B) at the insertion of a pair of leaves, *a* and *a′*, which had developed with a marked displacement to one side, and which showed, at the point of insertion only, an intimate fusion with one another. Bending of the axis was away from the side on which this basal union had taken place. Separation of the succeeding pair of leaves, *b* and *b′*, each of which subtended an axillary bud, had resulted in more distortion; the figure makes it clear that, although the distance between the insertions of *b* and *b′* was considerably smaller than that between the insertions of *b* and *a* (and of its partner *a′*), leaf *b* corresponded more closely developmentally to leaves *a* and *a′* than it did to leaf *b′*; together with them it had already begun to present the appearance of a trimerous whorl. In the same way leaf *b′* was more closely associated, both positionally and developmentally, with leaves *c* and *c′* than with its partner *b*.

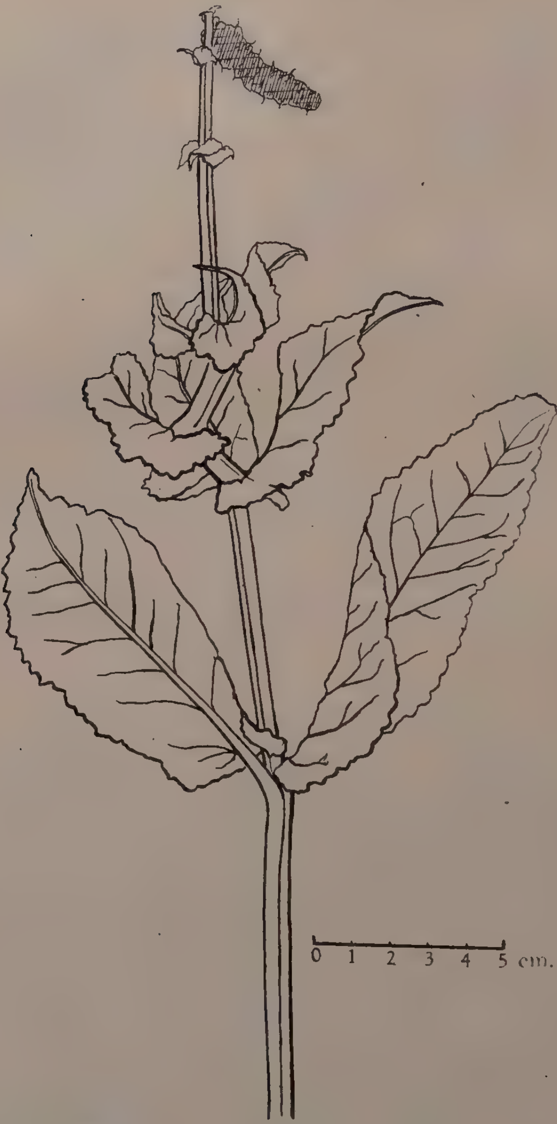


Text-fig. 6. A. Shoot E (*Salvia pratensis*), showing arrangement of leaf pairs. B. The same with the lower leaves dissected away.

Shoots F and G (*Salvia pratensis*)

In yet another atypical shoot of *Salvia pratensis* (shoot F, Text-fig. 7), the decussate arrangement had apparently again been modified by a failure of the normal binding process. Considering the leaves in acropetal succession, it will be seen from the figure that although the basal pair were inserted almost normally, they were somewhat displaced to one side and there was slight bending of the axis. At the level of insertion of the third and fourth leaves there was considerable distortion, and at the third node the single (fifth) leaf produced maximal bending of the axis (a bend, in fact, of almost 90°). There followed a node at which there was less disturbance, and at which three transitional leaves were inserted. At this point the stem became five-angled; trimery was fully established in the node above this, where flowering was beginning in the axils of each of three bracts. This trimery was maintained in the remainder of the shoot, now fully committed to flowering; but it must be emphasized that it was based, not on a typically jugate system, but on a phyllotactic system with a theoretical leaf divergence of 144°.

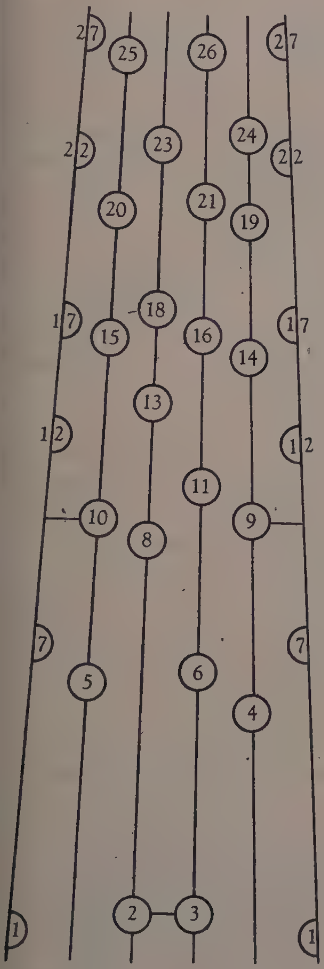
Details of the last shoot to be described in this series (shoot G, Text-figs. 8, 9) are included as a record of an abnormal shoot in which the leaf divergence was 144° from a very early stage, and in which the uneven operation of the 'binding factor' assumed above could be used to explain once again the ultimate development of a sequence of trimerous whorls in the flowering part of the shoot. The phyllotactic plan is laid out in Text-fig. 8. The radical leaves of the plants included one two-topped and one normal leaf. It will be noted from Text-fig. 8 that at this point there was a departure from the subsequently constant leaf divergence of 144°. About 15 cm. above this node were inserted three leaves, and the axis showed distortion, presumably in consequence of the spatial separation of the first of the leaves from the subsequent pair. This group was followed by a single leaf, with considerable disturbance of the axis at its point of insertion, then by a group of four leaves, shortly separated and occasioning much distortion; there followed two well separated leaves, also with much consequent distortion. Then came a nodal group of five closely associated leaves (showing transition to bracts), and in the subsequent node, 7½ cm. distant, trimery was established and continued thereafter unaltered throughout the flowering part of the shoot. Here, as in shoot F described above (Text-fig. 7), trimerous whorls were derived from a phyllotactic system with a theoretical leaf divergence of 144°, and were not, as seems to be the more generally reported case in members of the Labiatae showing trimery, the result of the establishment of a regular (3+3) system.



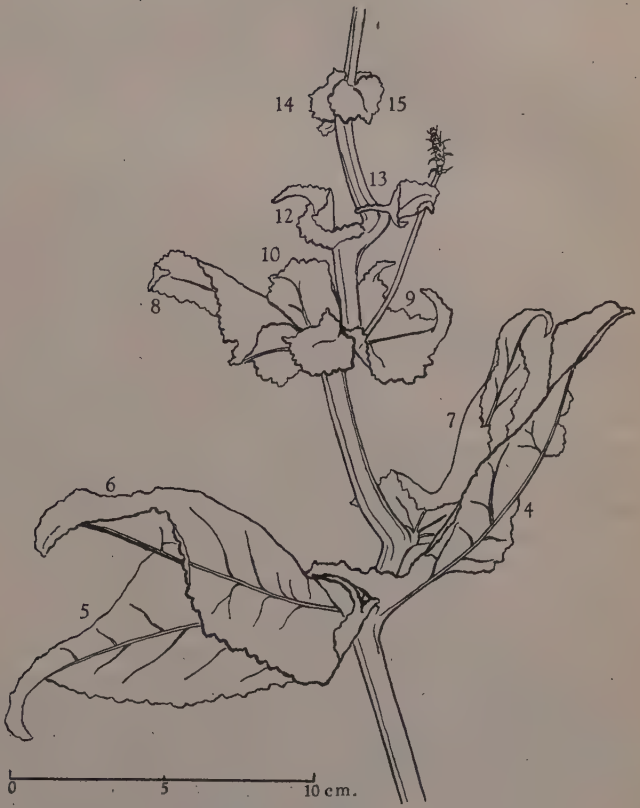
Text-fig. 7. Shoot F (*Salvia pratensis*).

General discussion

Several points of interest remain which call for brief discussion, though it need hardly be emphasized that many of the suggestions made here must remain largely speculative, until botanists are in a better position to analyse more closely the events which have their origins in the stem apex.



Text-fig. 8. Phyllotactic plan of shoot G.



Text-fig. 9. Lower part of shoot G (*Salvia pratensis*).

Distortion of the stem

The records of stem distortion in these aberrant forms give weight to the belief that growth is being stimulated locally wherever, through the failure of the assumed 'binding factor', paired leaves have become longitudinally separated. If one recalls the regular zigzag distortion of shoot A (Text-fig. 1), associated with the regular alternation of single- and two-topped bracts, it will be apparent that bending of the axis, being invariably in a direction away from the locus of insertion of the bracts, could be interpreted as the result of a downward diffusion of hormones from each bract, resulting in localized growth in the region of insertion.

Anatomical studies of some of the distorted nodes encountered in these shoots pointed fairly clearly to the fact that growth was due to an increase in meristematic activity rather than to a localized differential extension of tissues, of the type involved in auxin activity. Reference to Pl. **4**, fig. 1 will show the nature of the evidence upon which this statement is based. The first node of shoot E is shown in somewhat tangential longisection; it will be seen that parenchymatous cells of both cortex and medulla on the convex side of the bent stem were smaller in stature, and had been involved in more recent meristematic activity than those on the concave side of the stem. Shoot E (Text-fig. 6) showed that the growth effect at this node, and presumably at other nodes, was operative at a time when the leaf was rapidly expanding; it was completed before the leaf had achieved maturity. Longisections of a node of shoot F showed, furthermore, that bending had occurred after the differentiation of early protoxylem, since in the process of distortion whole protoxylem vessels had been bent back upon themselves (see Pl. **4**, fig. 2). There are, then, two approximate time limits within which this promotion of meristematic activity may have taken place, a feature which should later prove of value when an attempt is made to reproduce this phenomenon experimentally.

This extends and makes possible a physiological interpretation of the suggestion of Schoute (1938, p. 433) that: 'in some species with decussate leaves the growing leaf insertions develop strong displacing forces which are counterbalanced in the normal dimerous whorls, but cause a bend in the stem at a node with one leaf, and we may even say that in those species, the opportunity is used for developing the leaves at an earlier stage than usual, so that for a time they are stronger than the apex.'

It may thus be postulated that hormonic stimulation of meristematic activity has taken place in the region of the insertion of the leaves, and that the hormone involved is derived from the leaves themselves. The stimulation, furthermore, occurs at a period when the production of auxin is most probably on the wane (as reported by Avery (1935) for developing leaves of *Nicotiana*). This appears to be a fresh aspect of the many-times reported capacity of developing young leaves and buds for the stimulation of meristematic activity in dormant cambia and in other relatively undifferentiated tissues. Its main interest would seem to lie in the fact that it involves a hormone which acts, not perhaps independently of, but certainly in opposition to auxin, which should also be present and operative at this stage.

It is to be presumed that the factor is working also in normal plants of *Salvia*, when it would be responsible for some increase in nodal growth at a time when internodal elongation would gradually be coming to a standstill. As Schoute pointed out, it would not be obvious in such plants for the reason that the influences of opposite leaves will counterbalance each other; it only becomes apparent in these specimens of *Salvia* through the upsetting of the balance established between paired leaves, due to their separation in position along the stem.

The irregularity in operation of the hormone, as judged solely by the extent of stem distortion, must be the consequence of a number of modifying factors, of which only two or three may be mentioned here. If diffusion of the hormone from the leaves can take place to tissues around the greater part of the circumference of the stem, then one would not expect great distortion, since any growth stimulated thereby would be general and not unilateral, rather as when two opposite leaves cancel each other out in their effects. Examples of this can be seen in shoot B (Text-fig. 4A, node *a*); and again in shoot D. Moreover it is unlikely that the hormone will always be produced in similar concentrations from all leaves, and variation must be expected in this respect. Finally, it must be borne in mind that some correction of this type of bending may occur as the result of the normal (auxin-controlled) response of the stem to unilaterally operating gravitational stimuli.

The latter part of Schoute's statement, quoted above, is less easy to interpret, namely, 'that in those species the opportunity is used for developing the leaves at an earlier stage

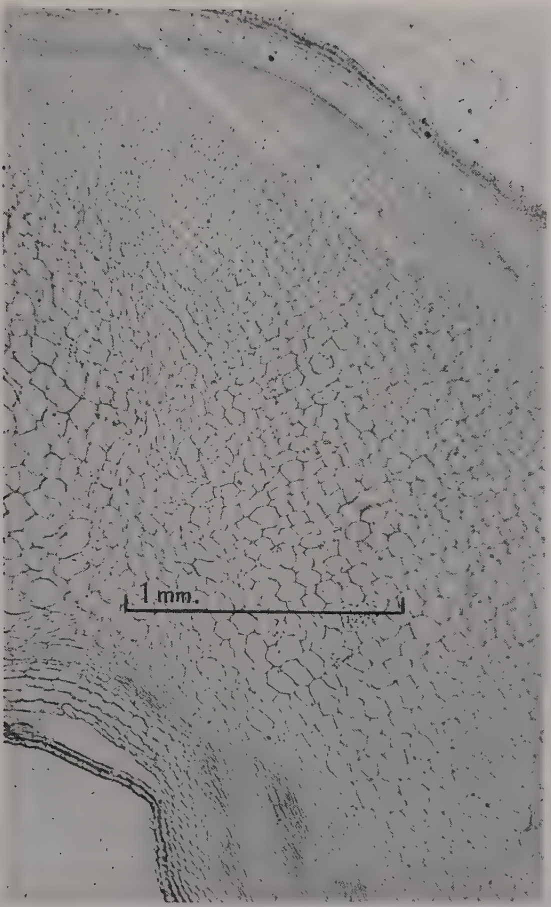


Fig. 1. Photo-micrograph of a tangential longisection through lowest node of shoot E. ×37.

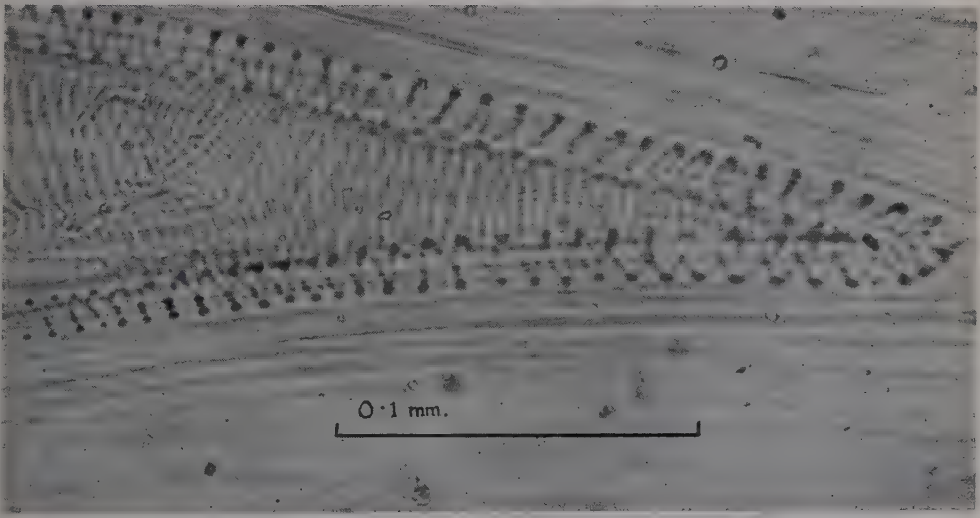


Fig. 2. Portion of radial longisection through a node of shoot F, showing the bending of early protoxylem vessels due to stem distortion. ×480.

than usual, so that for a time they are stronger than the apex'. It is well known that in most decussate plants the stem apex is relatively flattened, and that it is in effect overshadowed by the developing leaves which surround it. Plant physiologists are not yet technically in a position to assess the relative importance of stem apex and of leaf rudiments in the production of hormones, but it should be apparent that if, as is commonly supposed, hormone production is related to high metabolic activity in protein synthesis, then a rapidly developing leaf may overtop a less active apex in this respect. If stem apex is dominant in hormone production, as perhaps in most plants with alternate leaves, the localized diffusion of hormones from leaf to stem is less likely to produce such effects as have been observed here. It may be that in some plants protein metabolism is at a higher level of intensity in the young leaves than in their shoot apices. In other plants with a relatively more massive (and active) shoot apex, leaf activity may be relatively lower. This is suggested by the findings of Nightingale, Thomas and others (see review by Nightingale, 1937) that in some plants nitrogen metabolism is most intense, not in the leaves, but primarily in the young rootlets. It would plainly be of value to attempt to correlate hormone activity of the type reported with activity in the synthesis of proteins. Just as in certain plants with alternate leaves (e.g. *Tilia europea*) there is often some tendency to bending of the axis at the point of leaf insertion, so it may be expected that some, but not all, whorled plants will be alike in this respect. It is interesting to reflect that the decussate or whorled arrangement of leaves would offer a means to the attainment of stability in plants where such differential growth effects might otherwise constantly disturb normal orthotropous growth.

The nature of the 'binding factor'

Schoute's 'binding factor' may be visualized (again perhaps on a growth hormone hypothesis) as the outcome of an early maturation and commitment of the superficial tissues which separate recently induced leaf rudiments. Whilst such tissues remain meristematic and plastic, spatial separation of the rudiments is still possible, and is normally quite likely to occur; as a result, a normal spiral phyllotaxis may be developed and observed in the adult shoot. It is not unlikely that the phyllotactic system finally achieved will depend on the duration of this plastic phase. Whatever the real significance of phyllotactic systems in the adult shoot (and in relation to this see Salisbury (1931), p. 542), it seems to me that they may well be but the reflection of a greater or lesser prolongation of the meristematic activity of those superficial tissues not involved in the induction of leaf rudiments.

The phenomena that Schoute has ascribed to 'binding' certainly all point to some such explanation as this, and it remains to be seen how far this view can be justified in the light of what is known about auxin activity. It becomes more and more widely evident that growth hormones of the auxin type may have a multiplicity of effects, depending not only on their concentration, but presumably also on the physiological state of the tissues in which they are active. Thimann (1937) has shown the operation of the concentration principle in buds, stems and roots, and it is difficult to feel any doubt that the same general principle holds for all tissues.

Thus auxins may apparently promote or inhibit meristematic activity in a cell. Auxin-promoted meristematic activity has been postulated by some writers as the outcome of a stimulation of cells to the production of traumatin-like hormones by physiologically supernormal concentrations of auxin. (It is possible that this may be the source of the hormone which stimulates cell division in the instances of stem distortion discussed above.) In inhibiting cell division, however, auxins may help to urge a cell, not always irreversibly, past that point at which such activity becomes either likely or readily possible. Thus under suitable conditions auxins may apparently also promote the attainment of maturity in a cell, with its attendant phases of elongation, volume increase, and any subsequent differentiation which may occur. The work of Commoner & Mazia (1942) suggests how this may be achieved through the regulation of salt intake.

It is suggested here, then, that as the result of local regulation of auxin concentration at an early stage, associated with the early development of the leaf rudiments in relation to the stem apex, superficial tissues of the apex not involved in the original induction of leaf rudiments may become committed to the phase of maturation at an earlier stage than in plants where the leaf rudiments are less forward in their development. This presupposes that all tissues within the zones of leaf induction are in a physiologically different state from the residual superficial tissues of the stem apex; and in view of their subsequent direction of development, this belief is quite tenable.

It is of interest to recall that the experimental treatment, by Snow & Snow (1937), of the apices in plants of *Epilobium hirsutum* and *Lupinus albus* yielded results which could be explained on this view. Some sixteen or seventeen days after auxination, they found evidence, more particularly in *Lupinus*, of union between adjacent primordia; in two examples out of sixteen, three primordia were involved in fusion. They observed also a relative displacement of primordia towards the locus of auxination. I would regard both these results as due to a local restriction of cell division in the superficial tissues of the apex, leading to a more or less close association of the primordia. In *Lupinus* (but less so in *Epilobium*) the association was evidently close enough and early enough to result in union of the primordia. In *Epilobium*, the differential extension of residual superficial tissues seems to have led to a looser association, observed as a relative displacement of one primordium towards another.

Similar phyllotactic changes were observed by Ball (1944) in the shoot apices of *Tropaeolum majus* L., following the application to them of concentrated emulsions of synthetic growth substances. He recorded the association at one level of two, three and four leaves at a time, and, on occasion, the production of multiple fasciated leaves, whose axillary buds showed the characteristics of a fasciated apical shoot. Ball suggested that a high local concentration, artificially or naturally induced, may lead to a local rise in the concentration of nutrients. I would suggest the possibility that here also a high local concentration of hormone may affect differentially the rates of development of superficial leaf-rudiments and residual tissues at the apex, even if these are as yet visually undeclared.

Snow (1942), in a recent criticism of Schoute's theory, recognized the possible operation of two of the regulating factors postulated by the latter (viz. a factor for levelling of the insertions of the members of a whorl, and a factor for equalization of the angles of divergence between them); he found it difficult to accept the operation of such factors at levels above those of the youngest primordia.

It seems to me that to attempt an explanation of intimate leaf fusions in terms of the more or less close association of leaf initials, it may be necessary to conceive of this process as occurring in the pre-visual stage in the development of such initials. The modification of the angle of divergence between leaves, brought about experimentally both by the Snows and by Ball, may in some instances be due to the operation of factors for leaf association in the visual phase; but it is surely more likely that, whenever primordia not visible at the time of operation are displaced towards one another in subsequent growth, it is the result of occurrences in the pre-visual stages of development.

This view of the association of rudiments is not necessarily at variance with the view previously put forward to account for stem distortion. Borthwick, Hamner & Parker (1937) have shown that the histological response of stem tissues in tomato to treatment with heteroauxin is not the same in all tissues. Thus whilst parenchymatous tissues generally (and especially within a zone to a depth of from 0·5 to 2·0 mm. from the surface) responded by reversion to meristematic activity, epidermis was little affected in this respect, though like most other tissues it responded by elongation. In this present account it is supposed that leaf association is due primarily to the early maturation and commitment (beyond the stage in which meristematic activity may readily take place) of the epidermal tissue between leaf rudiments. Subsequent cell division in the underlying tissues as the result of hormone stimulation, will require only that these epidermal tissues should enlarge to accommodate the growth of the tissues beneath them.

Two-topped leaves

The production of two-topped leaves in *Salvia* has been figured and described on more than one occasion. Attention is drawn to it again in this communication merely to emphasize my belief that the views of Schoute on this point (1936, p. 675) are essentially correct. He thinks that the occurrence of two-topped leaves is to be expected in plants showing 'early binding whorls', and is the result of the induction of two leaf rudiments in such close proximity to one another that they may in the adult state have lost, more or less, their identity as individual leaves. Whilst the above concept of 'binding' may hold good, one is constantly reminded that there is as yet little real indication (apart from the work of Snow & Snow (1931 *et seq.*) on the positional aspect) as to the conditions and factors involved in the initial induction of a leaf rudiment at any one particular locus.

The special case of shoot A

In the light of this discussion on the 'binding factor' and of the production of two-topped leaves and bracts, the case of shoot A (*S. Verbenaca*) may be reconsidered. It was suggested earlier that if a 'binding factor' is involved here in the production of bifid bracts, it could be either sectorial in its operation with respect to the shoot apex, or it might function discontinuously. Sectorially operating factors are not unknown in other fields; thus sectorial chimaeras, which may in fact be mericlinal and not fully sectorial, are discussed in a review by Neilson Jones (1937). To quote a more recent and practical example, Dermen & Bain (1944) have demonstrated the experimental production of sectorial polyploidy by the colchicine treatment of cranberry shoots. So also in this shoot of *S. Verbenaca* it seems feasible that a sectorially operative factor may be present, which through auxin regulation achieves a limited unilateral linking of leaf or bract rudiments. If, as suggested, this is brought about by the inhibition or limitation of cell division in the epidermal tissue between adjacent leaf rudiments, then the earlier the modification of such tissue, the closer will be the linking of the developing leaves. Here is perhaps an instance of a stem apex essentially conforming to a production of leaves with a divergence of 1/3, in which one sector (120°) differs from the remaining two sectors (totalling 240°). The latter, coming under the influence of a regulating factor, may show close association of the bract pairs produced. The association is so close that their total physiological demands and effects are comparable to those of a single normal bract; it seems likely that the anatomical features observed are determined by these demands and effects, and result in the delimitation of the flattened stem which has been described.

SUMMARY

1. Seven abnormal shoots, three of *Salvia Verbenaca* and four of *S. pratensis*, are described with special reference to the deviation that they show in leaf insertion from the normal decussate arrangement; reference is also made to the distortion of the axis, and the fusion of leaves and bracts consequent upon this deviation.

2. Two instances are described of the establishment of trimerous whorls based on a theoretical leaf divergence of 144°.

3. Schoute's theory of binding whorls is discussed and extended in terms of growth hormone concepts and possible events at the shoot apex.

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A revised classification of Leptosporangiate ferns. By R. E. HOLTTUM, M.A., F.L.S.

[Read 9 May 1946]

In 1938 the late Carl Christensen published a sketch for a natural classification of ferns, prefacing it with a discussion of previous schemes of classification. This work of Christensen owed much to the morphological work of Bower, Goebel and others, but it owed more to the intensive knowledge acquired by its author during a lifetime of systematic study of ferns from all parts of the world. He probably had a more thorough knowledge of ferns than has been acquired by any other man, and his sketch of 1938 is of corresponding significance. He himself regarded it as no more than a tentative scheme, and frequently noted genera the limits or status of which were uncertain. It is, however, the best general survey of a very complex subject which has yet appeared, and one can only regret that Christensen himself did not live to publish a revision of it.

In 1942–44 I wrote at Singapore a fern flora of the Malay Peninsula, using Christensen's scheme as a basis for its arrangement. During the work I came across many facts which struck me as significant, and I gradually developed ideas for a modification of the scheme. The modified scheme so arrived at is here presented, with a discussion of the reasons for the changes made, and of the main evolutionary trends in each of the major groups. There are many matters that still call for study—indeed, one cannot even claim that all the major groupings are yet clear—but the present scheme is put forward in the hope that the new facts may be of value, and that the new arrangement may provoke criticism and ideas for further work from others who may be interested in the subject.

As regards relevant former literature, most of this is cited by Christensen in his *Index Filicum* (with supplements) and his paper of 1938; it is thus only necessary to cite here a few more recent papers, and some of special importance.

I have pleasure in expressing thanks to the Keeper of the Herbarium and his staff at Kew for help in reference to specimens and literature which enable me to add some further information not available in Singapore.

SUMMARY OF PROPOSED CHANGES

It has long been customary to include all Leptosporangiate ferns, other than those of a few well-marked more primitive families, in a comprehensive family Polypodiaceae. The primitive families are very thoroughly dealt with by Bower in *The Ferns*, vol. 2. Christensen in 1938 agreed in the main with Bower in delimiting these families, only removing *Dipteris* and *Dennstaedtia* to Polypodiaceae. I follow Christensen in this, and give no further discussion of the primitive families, confining my attention to Christensen's Polypodiaceae, which includes some 7000 species. This Christensen divided into fifteen subfamilies, 'though most of these are well characterized and were perhaps better dealt with as families'.

Some of Christensen's subfamilies are more nearly related together than others. In particular, his Polypodioideae and Dipteridoideae together form a very isolated group, which I suggest should constitute a distinct family; this must be called Polypodiaceae, since it includes the genus *Polypodium*. From this family I exclude *Grammitis* and allied genera, which Christensen already noted as not nearly allied to the true Polypodioid ferns. They seem equally unrelated to all the more advanced groups of Leptosporangiate ferns, and are therefore placed in a distinct family Grammitidaceae.

In studying Christensen's Dryopteridoideae, it seemed to me that too little stress had been laid on the differences of the *Thelypteris* group of genera from the *Dryopteris* group. It has been customary to regard all as of Cyatheoid origin; but I found evidence that

Dryopteris and its near allies are related to *Dennstaedtia*, not to *Cyathea*. This evidence does not apply to the *Thelypteris* group, which (as indicated by Christensen himself) appear to have no near relatives; I therefore constitute them tentatively a separate family Thelypteridaceae, which may be allied to Gleicheniaceae and Cyatheaceae.

All the remainder of Christensen's subfamilies, except Gymnogrammoideae, Vittarioideae and Onocleoideae, appear to be closely related together, with Dennstaedtioideae and Lindsayoideae as the most primitive groups and other subfamilies representing various different evolutionary lines. It appears reasonable to constitute this great assemblage one family, for which I propose the name Dennstaedtiaceae; it is by far the largest family in the new arrangement, and some changes in its division into subfamilies are proposed as compared with Christensen's scheme. One might also include *Dicksonia* and its near allies, as they are most probably closely related to *Dennstaedtia*. But it is probable that *Dicksonia* represents a dead end in evolution (the advance to modern ferns came, as I see it, in all cases from ancestors with creeping dorsiventral rhizome) and I prefer to leave Dicksoniaceae as a separate family of primitive ferns.

As regards Gymnogrammoideae, opinions are somewhat divided, and I have little new to add. I provisionally rank them, with the probably allied Vittarioideae, as a separate family, to which I give the name Adiantaceae, as *Adiantum* is one of the largest and most distinctive genera in it, whereas *Gymnogramme*, in its modern restricted sense, is neither large nor distinctive. I add *Taenitis* to this family, and give some discussion on this and allied Malaysian genera.

There remains Christensen's Onocleoideae, concerning which I have nothing new to add. As indicated under the discussion of *Blechnum*, I do not accept this as a group intermediate between Cyatheaceae and *Blechnum*. I doubt whether it is nearly related either to Cyatheaceae or to Dicksoniaceae, and leave it at present unplaced, pending further investigation. The revised scheme of families is then as follows.

Family POLYPODIACEAE

Polypodioideae C.Chr. (excluding *Grammitis*, etc.) and Dipteridoideae C.Chr.

Family GRAMMITIDACEAE

Grammitis and allied genera (placed by C.Chr. at end of Polypodioideae).

Family THELYPTERIDACEAE

Thelypteris, *Cyclosorus*, *Goniopteris*, *Meniscium*, *Glaphyropteris*, *Steiropteris*, *Dictyocline* (but not *Gymnocarpium*, *Pteridrys* and *Monachosorum*, transferred to Dennstaedtiaceae).

Family DENNSTAEDTIACEAE

1. Dennstaedtioideae C.Chr. with addition of *Culcita* and *Monachosorum*.
2. Lindsayoideae C.Chr. with exclusion of *Taenitis* (transferred to Adiantaceae), *Diellia* (to Oleandroideae), and *Dictyoxiphium* (to Tectarioideae).
3. Davallioideae C.Chr. with addition of *Rumohra* (sens. strict.) and exclusion of *Nephrolepis*, *Arthropteris* and *Psammisorus* (transferred to Oleandroideae).
4. Oleandroideae C.Chr. with addition of *Nephrolepis*, *Arthropteris*, *Psammisorus*, and *Diellia*.
5. Pteridoideae C.Chr. (including Acrostichoid genera).
6. Asplenioideae: Asplenioideae § Asplenieae of C.Chr. only.
7. Blechnoideae C.Chr.
8. Lomariopsidoideae: *Egenolfia*, *Bolbitis*, *Lomariopsis*, *Thysanosoria*, *Teratophyllum*, *Lomagramma*, *Elaphoglossum*.
9. Dryopteridoideae: *Woodsia*; *Stenolepia*, *Acrophorus*, *Diacalpe*, *Peranema*, *Lithostegia*; *Dryopteris*, *Polystichum*, *Polystichopsis*, *Cyrtomium*, *Didymochlaena*, *Gymnocarpium* (also *Maxonia* and *Polybotrya*?).

10. Tectarioideae: (*a*) *Ctenitis*, *Lastreopsis*, *Tectaria*, *Heterogonium*, *Quercifilix*, *Stenosemia*, *Hemigramma*, *Amphiblestra*, *Pleuroderris*, *Dictyoxiphium*, *Cyclopeltis*; (*b*) *Pteridrys*, *Pleocnemia*, *Arcypteris* (*Dictyopteris* Presl non Lamx.).
11. Athyrioideae: *Athyrium* (including *Diplazium*), *Cystopteris*.

Family ADIANTACEAE

1. Gymnogrammoideae C.Chr. with addition of *Taenitis*.
2. Vittarioideae C.Chr.

Unplaced: Onocleoideae C.Chr.

Bower divided Leptosporangiate ferns into Superficiales, derived from Gleicheniaceae, and Marginales, derived from Schizaeaceae. He included in Marginales subfamilies 1–5 of Dennstaedtiaceae as above arranged, but subfamilies 6, 7, 9, 10, 11 he ranked as Superficiales. The crucial subfamilies are nos. 6 and 9, under each of which the reasons for their change of position are given. There can be little doubt that nos. 10 and 11 are related to no. 9; the position of no. 7 is more doubtful. As regards no. 8, Bower does not present the facts at all fully; Christensen is more explicit, but I give reasons for differing from him in placing the subfamily, and add *Elaphoglossum* to it (placed by Christensen in a separate subfamily).

Copeland (1929, 1941) has criticized other proposals to subdivide the traditional Polypodiaceae, and himself includes in it some of the more primitive families, on the ground that the whole assemblage is one phylum and that to separate as families some groups of genera because they retain more primitive features is unnatural. He is also of the opinion that any families formed by subdivision of the traditional Polypodiaceae would be unstable because they could not be precisely defined. With Copeland's criticisms of Ching's scheme (1940), in which the old Polypodiaceae is divided into thirty-three families, I am in general agreement; but I suggest that a middle course such as here attempted is possible and reasonable. Though the largest family Dennstaedtiaceae is not definable in words, its subfamilies are reasonably definable; and it seems to me that there is good evidence to show that these subfamilies are more nearly related together than any of them are to the groups segregated as Polypodiaceae, Thelypteridaceae, Grammitidaceae and Adiantaceae. Copeland's argument could be used to make one family of all Dicotyledons.

Family POLYPODIACEAE

General characters

Rhizome creeping, usually epiphytic, containing (as seen in section) a ring of small vascular strands, or a solenostele in a few primitive genera, externally scaly; *scales* peltate at the base (hairs present only in *Dipteris* and *Cheiropleuria*).

Fronds two-ranked, on the upper side of the rhizome and nearly always jointed to it, simple and entire, or more or less deeply lobed, or pinnate; *veins* reticulate with free veins in the areoles or rarely all free.

Sori without indusia (though sometimes protected when young by peltate paraphyses), *either* almost round, small or large, sometimes sunk in cavities in the surface of the frond, on free or connected veins, or on a plexus of veins; *or* elongated parallel to the main veins; *or* elongated parallel to the margin; *or* acrostichoid on part or all of the frond.

Spores without perispore, bilateral.

The primitive existing genus of the family is *Dipteris*, characterized by bristly terrestrial solenostelic rhizome, fan-shaped frond with main veins repeatedly forked catadromically at the base, smaller veins arising pinnately from the main veins or their branches, still smaller veins forming an elaborate network with many short free veins in the areoles, and small to medium-sized sori, with paraphyses but without indusia, with tendency to a 'mixed' condition. *Dipteris* is closely allied to Mesozoic fossil ferns of similar frond-form and venation. In contrast to other families of Leptosporangiate ferns, a fully reticulate venation thus developed very early in its history. An interesting parallel case of quite similar venation is Christensenia (Marattiaceae), the antiquity of which is unknown, but which shows that elaborate anastomosis of veins could develop in ferns of otherwise primitive character.

The primary catadromic (unequally dichotomous) branching of the veins is a character found in no other group of ferns except Matoniaceae, for which reason *Dipteris* and *Matonia* have usually been associated together. It may well be that they had a common origin; but they must have diverged at an early stage, *Matonia* developing only slight anastomosis of veins and retaining large sporangia with a distinctive indusium, *Dipteris* developing elaborate anastomosis and smaller sporangia without indusia. I suggest therefore that it is well to maintain Matoniaceae as a distinct family. Bower states that *Dipteris* and *Matonia* differ in the primary branching of their veins, that of *Dipteris* being anadromous and that of *Matonia* catadromous; but, as pointed out by Posthumus, this is merely due to a twisting of the halves of the frond of *Dipteris* which commonly occurs when they are flattened for mounting.

As shown below, the dichotomous branching of the main veins disappears in the majority of members of Polypodiaceae, but the *Dipteris*-form of reticulation of the smaller veins persists throughout the majority of genera, and is to be regarded as the primitive state of the family as here limited. Apart from *Christensenia*, a comparable venation occurs only in *Tectaria* and *Bolbitis*, in which it undoubtedly developed late, on entirely distinct lines of evolution. Some species of *Tectaria* and *Polypodium* (sens. lat.) are so much alike in frond-form and venation that they have been placed in the wrong genus, but their fundamental difference is seen in scales, rhizome-anatomy and spores. In the same way, Copeland has asserted a relationship between *Bolbitis* and *Polypodium*, but in my view this is disproved by spores and anatomy.

Bower has described in detail the series *Dipteris*, *Cheiropleuria* and *Platycerium* (*The Ferns*, vol. 3, ch. XLV); he has also described *Neocheiropteris*, a link between *Dipteris* and the reticulate-veined species of *Polypodium* (sens. lat.), some of which (a rather haphazard collection) have also been dealt with by Goebel (*Ann. Buitenz.* vol. 36). But neither author seems to have seen the full implication of their work, apparently through lack of acquaintance with the species of Polypodiaceae.

The presence of peltate scales on the rhizome, and stellate hairs or peltate scales on the fronds, is characteristic of almost all Polypodiaceae except *Dipteris* and *Cheiropleuria*, which have bristly or hairy rhizomes. As shown by Bower, the evolution of peltate scales from stellate hairs is a simple one. The more primitive condition of stellate hairs on the fronds (also covering the young sori) is seen in *Platycerium*, *Cyclophorus* and *Drymoglossum*, which all have peltate rhizome scales (Bower states that *Platycerium* has a hairy rhizome but figures part of a scale on p. 220). The other genera mostly have peltate scales on their fronds, in some cases very few and early deciduous.

We must thus postulate a fern with stellate hairs as the common ancestor of all but the most primitive Polypodiaceae. Such an ancestor must also have had a frond-form with branching of the main veins as in *Dipteris*. Among existing ferns the only genus combining these characters is *Platycerium*, but this is evidently a very specialized genus which is not on the main line of evolution of the majority of Polypodiaceae. Among ferns with peltate scales on their fronds, the most primitive in frond-form is *Neocheiropteris palmatopedata*. This has the main veins branched at the base as in *Dipteris*, and fairly large sori, protected by peltate scales, each sorus seated on a small plexus of veins.

If *Neocheiropteris* produced offspring with simple unlobed fronds (see Ching, 1933), they would exactly resemble *Lepisorus*, and it is most probable that *Lepisorus* originated in this way. The production of a simple frond from the pedately lobed *Dipteris-Neocheiropteris* type seems to me a main step in the evolution of Polypodiaceae.

Having produced the simple frond, with a single row of large sori (protected by peltate scales) on each side of the midrib, the sori separated by main veins, several further changes become possible. The sori only develop in the apical part of the frond, which becomes narrow so that the sori cover it completely, and we have *Hymenolepis*. The sori increase in number and lose their peltate paraphyses, and we have *Microsorium*. The main veins become strengthened and a lobe develops opposite each (as on the lobes of the frond of *Dipteris conjugata*), the frond becomes leathery, and we have *Phymatodes*. (*Pleopeltis*, in the strict sense, almost exclusively American, with peltate scales covering the fronds, perhaps had an origin separate from that of *Lepisorus*).

Another probable development from *Lepisorus* is *Loxogramme*, with elongate oblique sori between the main veins. This has lost the articulation of the fronds to the rhizome; or it might have been derived direct from a terrestrial fern which had not yet acquired this character (*Dipteris* fronds are not jointed to the rhizome).

From *Microsorium* we can derive *Colysis*, by spreading and fusion of the sori between the main veins; and from *Colysis*, by contraction of the fertile frond, we can derive *Leptochilus*. From *Microsorium musifolium*, with its very broad-based fronds and conspicuous venation, we can derive the *Drynaria* group, astonishingly diversified and remarkably adapted to epiphytic life. Yet the series *M. musifolium* to *Aglaomorpha heraclea* and thence separately to *Drynaria* and to *Merinthosorus* has no serious gaps in it. *Photinopteris* is more specialized.

Phymatodes is a fairly large and diversified genus, mainly Asiatic and Polynesian. From it various specialized groups have developed. *Lecanopteris* has a fleshy rhizome, ant-inhabited. *Selliguea* has elongate sori (possibly derived by fusion) between the main veins, an exactly similar development to that of *Colysis* but on a different evolutionary line. *Pycnoloma* and *Grammatopteridium* are small ferns with very narrow fertile fronds, the sori continuous on each side of the midrib. *Arthromeris* is a small genus in which the fronds are fully pinnate with articulated pinnae.

Some Asiatic species of *Phymatodes* with rather simple venation bridge the gap between *Phymatodes* and *Polypodium* (including *Goniophlebium*). The tropical members of this latter genus have anastomosing veins with each sorus terminal on a free vein within an areole, the areoles in regular series between costa and margin. (*P. verrucosum* has small scales, which are almost peltate, covering the sori, much as in *Lepisorus*, a survival of a feature lost by *Phymatodes*.) The temperate *P. vulgare* and a few others have a simplified form of venation, with all (or nearly all) veins free. They are outliers of a predominantly tropical group. Probably also the same simplification has taken place among tropical ferns; there are Malaysian species with free veins which in other respects resemble *Polypodium* or *Phymatodes*, and their status needs further investigation.

There remain two genera to be considered, *Cyclophorus* (also called *Niphobolus* and *Pyrrhosia*) and *Drymoglossum*, ferns with simple fronds covered more or less densely with stellate hairs. There is little doubt that these have a common origin with *Platycerium*; and like *Platycerium*, though in quite different ways, they are remarkably adapted to epiphytic life (see Giesenhagen's monograph on *Niphobolus*). It is perhaps significant that some Chinese species of *Cyclophorus* have repeatedly dichotomous fronds.

The above generic names are those used by Christensen. In some cases the genera have not yet been clearly defined, and much yet remains to be done to stabilize them. It may be that not all will stand, or that some may be united and others again subdivided. As Copeland justly remarks, genera *must* be natural, and *should* be convenient. I believe that convenience is best served by making genera as large as possible consistent with a sufficient uniformity for the formation of a mental concept of the genus. The application of the principle is however not easy, especially in Polypodiaceae.

Owing to the absence of an indusium, soral shape and size in Polypodiaceae are very fluid, the sori tending to spread along the veins and to join in various ways. According to the Hookerian scheme, genera depended only on the form of their sori, and so the peculiar soral forms in this family received generic distinction, whereas the vegetative forms did not. We are still under the sway of this concept of the primary importance of soral shape for classification; and so we recognize *Selliguea* as a genus distinct from *Phymatodes*. But *Selliguea* is more nearly related to some species of *Phymatodes* than the latter are, say, to *Lepisorus*, or even perhaps to some other species which, because of their round sori, might rank as *Phymatodes*. The question then is, whether to try to subdivide *Phymatodes*, including *Selliguea* in that group of *Phymatodes* from which it was probably derived, or whether to be content with cutting off *Selliguea* on the convenient ground of its long sori. The former process is the more natural one, but is much the more difficult, and our knowledge is at present insufficient to carry it out (see Christensen, *Dansk Bot. Ark.* vol. 5, no. 3, 1929).

In Polypodiaceae we thus have an entirely different evolutionary development in frond-form and venation from that of other families. The primitive Polypodiaceae have pedate-dichotomous branching of main veins and lamina, with a distinctive form of reticulation of the smaller veins. Next we have the dichotomous frond reduced to a simple lamina, probably toothed at the edges as in the lobes of *Dipteris conjugata*. From this, pinnately lobed fronds, and ultimately (in *Arthromeris* and *Polypodium*) simply pinnate fronds, were evolved, in almost all cases except *Polypodium* with retention of the original type of reticulate venation. In tropical *Polypodium* the venation is modified (with transition forms now included in *Phymatodes*) and in a few species, including *P. vulgare*, the veins are free.

In the other families of ferns the sequence is always from free-veined bipinnate (or more amply divided) fronds to simple fronds with reticulate veins. In rare cases of extreme reduction (*Monogramme*) the free-veined condition may again be developed. In the Polypodiaceae, by contrast, the primitive members have elaborately reticulate veins and dichotomously branched fronds, leading to simple fronds and from these to pinnate fronds, ultimately by reduction, with free veins. The invariable creeping habit of Polypodiaceae, with fronds in two ranks, is a contrast to the other families, in which upright stocks have developed, often on several distinct lines.

Family GRAMMITIDACEAE

GENERAL CHARACTERS

Rhizome usually epiphytic, creeping or more or less ascending, in most cases (always?) dorsiventral in structure, with stipes alternating in two close ranks; vascular system a simple or somewhat dissected solenostele; *scales* usually brown, concolorous, cell-walls all uniform (superficial and lateral), base more or less peltate, edges often with stiff unicellular bristles.

Stipes jointed to rhizome or not, in some cases (all?) with a single vascular strand; stipes and frond usually bearing short or long stiff unicellular hairs or multicellular hairs with slender unicellular outgrowths.

Fronds either simple or more or less deeply pinnatifid to pinnate, rarely to bipinnatifid; *veins* free or in simple fronds with occasional anastomosis, usually simply pinnate in the pinnae of pinnate fronds.

Sori round or more or less elongate along the veins, without indusia, superficial or more or less immersed in cavities which are sometimes extended into grooves.

Sporangia naked or bearing stiff unicellular hairs; *spores* tetrahedral.

GENERA: *Grammitis, Ctenopteris, Prosaptia, Cryptosorus, Calymmodon, Cochlidium, Scleroglossum, Nematopteris.*

Because of their creeping rhizome, pinnate fronds with free veins and naked sori, the species now called *Ctenopteris* were long associated with *Polypodium vulgare*, and were often included in a group called EUPOLYPODIUM. Christensen has pointed out that the true relationship of *P. vulgare* is with the tropical ferns commonly called *Goniophlebium*, and that *Ctenopteris* is not nearly related. He cannot suggest a near relative for *Ctenopteris* and its allies in his Polypodioideae.

In view of the argument presented above concerning evolution within Polypodiaceae, it has long seemed to me that if *Ctenopteris* and its allies are Polypodioid ferns, they must represent a highly evolved and reduced condition, not a primitive one such as is assumed by Copeland. But in view of their lack of obvious relationship with any of the true Polypodioids, their abundant representation in the tropics of both Old and New Worlds, and their own peculiar characters, it seems to me preferable to regard them as constituting a distinct family.

Grammitidaceae are nearly all smaller than most Polypodioids; they have simpler vascular anatomy of rhizome and stipe; the stipes are frequently not jointed to the rhizome; they have stiff unicellular hairs on scales, frond-surfaces and often on sporangia (in some cases also on prothalli); they have (in all the many species examined by me) tetrahedral spores in contrast to the bilateral spores of true Polypodioids. The vascular structure has been examined in few species (Bower gives some data for a *Prosaptia*), and many are so small that its examination is difficult from dried specimens, which alone in most cases are available. Through the courtesy of Dr H. Hamshaw Thomas, I have examined material in alcohol of *Polypodium asplenifolium* Linn. (a *Ctenopteris*) collected by him in Jamaica. In this the stele of the rhizome is more dissected than a simple solenostele, and the stipe has a single vascular strand in which the xylem (as seen in cross section) has two divergent arms each ending in a protoxylem group. So far as I know, all true Polypodioids except the primitive *Dipteris* group have a much-dissected rhizome-stele appearing in cross section as a ring of almost equal small bundles, and several small bundles in the stipe. It seems fairly certain that simple vascular structure, the presence of unicellular hairs (or hair-branches) and tetrahedral spores are characters which distinguish these ferns from true Polypodiaceae.

Regarding Grammitidaceae as a fairly old group, numerous and widely dispersed but without near relatives among the more advanced leptosporangiate ferns, one may expect to find its nearest relatives among the more primitive families. The idea occurs to me that, like Thelypteridaceae, Grammitidaceae may be related to Gleicheniaceae, with which they agree in tetrahedral spores. In their stiff unicellular hairs on scales, fronds and sporangia they agree with Thelypteridaceae, but they differ so much in other characters that I do not think the two families are very nearly related, though both may originate from Gleicheniaceae. Much more information on the details of anatomy and form, and developmental studies, of the Grammitidaceae are however needed before one can make any reasonably definite statement about relationships.

The first genus of the family to receive a name was *Grammitis* (Swartz, 1801). As pointed out by Christensen, there is no very sharp distinction between *Grammitis* as representing ferns with simple fronds and *Ctenopteris* with pinnate ones. Several other genera (*Prosaptia* etc.) are so closely allied that they also are not very sharply distinct, and it would be defensible to include all in a single genus *Grammitis*. This would also simplify some problems of nomenclature, one of which is the status of the name *Ctenopteris*.

There are a few additional more specialized genera (*Cochlidium*, *Scleroglossum* and *Nematopteris*) which have simple narrow fronds and elongated sori near edges or midrib, often in grooves, for which reason they were formerly associated with *Vittaria*. They have been dealt with in a small monograph by Christensen (1929).

Goebel (1926) has an interesting note that two ferns of the *Grammitis* group (*Polypodium obliquatum* and *Prosaptia contigua*) have fronds which rest temporarily from apical growth, and resume it again; I have not myself noticed this, and it is perhaps less obvious in the less seasonal climate of Malaya than in Java. Certainly few ferns have this power; and conspicuous among them is *Gleichenia*, the fronds of which always rest from apical growth while successive pairs of pinnae are formed. This resemblance in behaviour between *Grammitis* and *Gleichenia* may be significant.

Family THELYPTERIDACEAE

GENERAL CHARACTERS

Rhizome creeping or suberect, not dorsiventral but bearing fronds and roots on all sides; vascular system a simple dictyostele.

Scales usually narrow, bearing stiff unicellular hairs on edges and surfaces.

Stipes containing two vascular strands at the base, uniting upwards to a single strand U-shaped in section.

Fronds usually pinnate-bipinnatifid, sometimes bipinnate, always much longer than wide, the lowest pinnae never much larger than the next and sometimes reduced; *pinnae* usually at a broad angle to the rachis, rarely very unequal at the base; *costules* at a broad angle to the costa, the veins in each lobe pinnate, *veinlets* usually simple but sometimes forked; a short or long translucent *membrane* usually present at the base of a sinus between two lobes, the veinlets of adjacent groups often joining the membrane, or joining to form an excurrent vein which meets the membrane; or where the pinna is hardly lobed veinlets of adjacent groups meeting and forming free or anastomosing excurrent veins; unicellular stiff *hairs*, and sometimes glandular hairs, present on surfaces of rachis, costa, veins and lamina, variously distributed.

Sori usually dorsal on the veins, round, with a reniform indusium (sometimes very reduced) or no indusium; in the latter case sometimes spreading a little along the veins, and the sporangia often setose.

Sporangia usually bearing glandular hairs on their stalks, and sometimes glandular cells or setae on their surface. *Spores* bilateral or rarely tetrahedral, with a winged perispore, or the wings more or less broken up into small laminae or spines.

Christensen included *Thelypteris* and allied genera as a separate group in his subfamily Dryopteridoideae, remarking that they are quite distinct from Dryopteris, and 'without near relatives outside the subfamily'.

Thelypteris is distinct from *Dryopteris* in its hairy scales and the similar hairs on frond-surfaces, in vascular anatomy, in frond-form, in the presence of the sinus-membrane and in venation. The features it has in common with *Dryopteris* are reniform indusia and spores with perispore. In view of the very great differences between the two genera, the possibility should be considered that these resemblances are due to convergent evolution, not to a common origin of the two genera. A reniform indusium has certainly developed independently in *Nephrolepis* and *Dryopteris*; why not again in *Thelypteris*?

Bower puts forward a theory of the origin of *Dryopteris* and its allies (he does not distinguish the *Thelypteris* group) from Cyatheaceae. Arguments are given below (under Dennstaedtiaceae, subfamily Dryopteridoideae) showing that this origin for *Dryopteris* is improbable; but these do not exclude the possibility of such an origin for *Thelypteris*, and this in fact appears quite probable.

Bower's thesis is that Cyatheaceae were derived from Gleicheniaceae, an intermediate being *Lophosoria*. The primitive *Gleichenia* leaf-form, seen in *G. glauca* and its allies, is very near to that of *Cyathea*, with pinnules nearly at right angles to the pinnae, veins pinnate in the lobes and the basiscopic side of basal pinnae not enlarged. The great differences between such a *Gleichenia* and *Cyathea* are: creeping rhizome, frond growing in stages (the apex resting while each pair of pinnae is produced) and fewer more primitive sporangia all developing simultaneously. Scales have already appeared in Gleicheniaceae, and the Cyatheoid scales are quite similar. Bower's suggestion of the development of the *Cyathea* indusium from a scale of the type found on the frond seems quite probable, and would explain the origin of an indusium in ferns derived from the exindusiate *Gleichenia* stock.

As regards rhizome, *Lophosoria*, with short erect trunk and solenostelic runners, bridges the gap between creeping and erect habit. The discontinuous growth of the frond of *Gleichenia* is a character which has also developed in *Dennstaedtia* and *Hypolepis*, and has been lost in the genera derived from them. The soral advance in Cyatheaceae is paralleled on other evolutionary lines, and is the kind of development we should expect.

The development of Cyatheaceae from Gleicheniaceae is then a probable one. If such an evolutionary change could happen once, it could happen again; and I suggest that *Thelypteris* perhaps originated from Gleicheniaceae, not by way of *Cyathea*, but independently on another evolutionary line. Let us consider in turn the characteristic features of *Thelypteris*.

SCALES AND HAIRS. *Thelypteris* scales all have many slender unicellular hairs, not only on their margins but usually also on their surfaces. *Gleichenia* scales, derived from branched hairs, have stiff unicellular marginal hairs, though not superficial ones. The appearance of superficial hairs seems possible as a later development. *Gleichenia* fronds bear usually branched or stellate hairs on their surfaces. A reduction of such to a unicellular state is surely possible; the stiff cells forming their branches are not unlike the unicellular hairs of *Thelypteris*. In *Goniopteris* the hairs are branched, but still unicellular.

FROND-FORM. The frond-form of *Thelypteris* is quite like that of some species of *Gleichenia*. I suggest that the most primitive existing species of *Thelypteris* is *T. ornata* of India and China, which has bipinnate fronds up to 6 m. tall. They would match well with the form of *Gleichenia glauca*. *Thelypteris brunnea* is closely allied but smaller, and it has varieties which are bipinnatifid, showing a complete gradation to the more usual smaller *Thelypteris* frond. This bipinnatifid frond is in shape very like a pinna of *Gleichenia glauca*; it has pinnae nearly symmetrical at their base, with lobes nearly at right angles and pinnate veins in the lobes; and it has a small translucent membrane at the base of the sinus.

SINUS-MEMBRANE. This sinus-membrane is a universal character in *Thelypteris* proper and *Cyclosorus*, though almost lost in the more highly evolved species called *Abacopteris* by Ching. A similar sinus-membrane is clearly seen in *Gleichenia linearis*, *G. Norrisii* and other species. In *G. linearis* the basal veins of adjacent lobes end at the sides of the membrane, very much as in some species of *Thelypteris*. There is a similar small membrane in some ferns of the *Tectaria* and *Dryopteris* tribes, but it is never so much developed.

SORI. The sori of *Thelypteris* are round, and seated upon the veins as in *Gleichenia*. They have often many sporangia, and are 'mixed'; the sporangia have the usual vertical interrupted annulus of advanced leptosporangiate ferns. Paraphyses often accompany the sporangia, or short hairs attached to the stalks of the sporangia, often ending in glandular cells. (The body of the sporangium sometimes bears unicellular hairs or glands like those on the leaf-surface.) Paraphyses also occur in some species of *Gleichenia*.

An indusium is present in most species of *Thelypteris*, but in some it is very small, and in others quite absent. The well-developed indusia are regular and firm, often bearing hairs on their surface and edges like those on the scales and fronds, or sometimes glandular cells (where such occur on the frond-surface). Bower (*The Ferns*, vol. 3, pp. 116–17) suggests the probability that the indusia of Cyatheaceae have originated from dermal scales or from fusion of paraphyses. If this could happen in *Cyathea*, it could happen in *Thelypteris*, the indusium here taking a different form. The reniform *Thelypteris* indusium could certainly develop from a basal scale such as that of the Cyatheoid ferns called *Hemitelia*.

SPORES. Thelypteris spores have (in nearly all cases) a perispore, which in *Thelypteris* proper appears to be always continuous and broadly winged, while in those species with anastomosing veins (called *Cyclosorus* by Christensen and Ching), there is a tendency for the continuous wing to break up into small parts, and these to be reduced to spines. (A similar tendency appears in *Lomariopsis*, certainly on a different line of evolution.)

A winged perispore occurs in several of the tribes of Dennstaedtiaceae (*Asplenium*, *Dryopteris*, *Athyrium*, *Tectaria* and *Lomariopsis* tribes) but not in the primitive ferns of that family, nor in the *Davallia*, *Nephrolepis* and *Pteris* tribes. A perispore does not occur in Adiantaceae nor in Polypodiaceae (sens. strict.). If we postulate an origin of *Thelypteris* from *Gleichenia*, a necessary corollary is that a perispore has originated independently in the two families Dennstaedtiaceae and Thelypteridaceae. I believe that it originated independently on more than one evolutionary line in Dennstaedtiaceae, and here put forward the theory that *Asplenium* is more nearly allied to *Davallia* than it is to *Athyrium* and *Dryopteris*. The development of a perispore from the disintegrated substance of the tapetal cells surrounding the developing spores is evidently not a difficult achievement, and quite probably originated more than once. A comparison of the perispores of *Dryopteris* and *Thelypteris* with high powers of the microscope and microchemical or other analytic methods might yield interesting results.

The genera of Thelypteridaceae

Christensen gives the following genera: *Thelypteris, Gymnocarpium, Glaphyropteris, Steiropteris, Pteridrys, Monachosorum, Cyclosorus, Goniopteris, Meniscium.*

GYMNOCARPIUM has the rachis-pinnule characters of *Dryopteris* and its immediate allies, and scales like *Dryopteris*, for which reasons a relationship to *Dryopteris* is indicated, though GYMNOCARPIUM has a simpler anatomy than *Dryopteris* and a creeping apparently dorsiventral rhizome. In any event, it is not near to THELYPTERIS, and needs further investigation. PTERIDRYS has the anatomy, venation and hairs (when present) of the *Tectaria* tribe, and I believe it to be allied to *Pleocnemia*; it is certainly nothing like *Thelypteris*.

MONACHOSORUM is placed by Diels and Bower near *Dennstaedtia*. It has a hairy solenostelic rhizome like that of the *Dennstaedtia* tribe, and in leaflet-form is much nearer to that tribe than to *Thelypteris*, with which it has very little in common. I think there can be no doubt of its exclusion from the present family.

The other genera are certainly closely allied together, and *Dictyocline* should be added to them. Christensen has dealt fully with the American genera in his monograph; I have no further information upon them. The Asiatic *Thelypteris* and *Cyclosorus* are however well represented in Malaya, and study of them has produced some data which may be summarized here.

Thelypteris is distinguished from *Cyclosorus* (according to Christensen) by having basal veins not running to the bottom of the sinus between segments, whereas in *Cyclosorus* the veins do run to the sinus, often uniting first to form a single excurrent vein. But in the species *Cyclosorus extensus* a single frond may show *Thelypteris* character on some pinnae, *Cyclosorus* character on others; and other species also are not clearly referable to one genus or the other. Further, it is certain that, disregarding these doubtful cases, there are relationships between groups of species in *Thelypteris* with groups of species in *Cyclosorus*; that is, certain species of *Thelypteris* are probably nearer to the corresponding group in *Cyclosorus* than to other species of *Thelypteris*. For example, *C. parasiticus* and allied species are related to *Thelypteris repens*, *T. Esquirolii* etc.; *Cyclosorus unitus* and *C. extensus* are probably related to *Thelypteris immersa*; *Cyclosorus gongylodes* may be allied to *Thelypteris crassifolia*; the group of *T. falciloba* with many auricles on the stipe, is probably related to some species of *Cyclosorus* which have the same character.

In view of these cross-relationships, I suggest that *Thelypteris* and *Cyclosorus* should be united in one genus (*Thelypteris*); this could then probably be subdivided on such characters as shape of frond, presence of reduced pinnae on stipes, glands on the frond and sporangia, and spores. I have attempted a grouping of Malayan species on such characters of *Cyclosorus*. They certainly indicate relationships, but are probably not sufficiently clear-cut to be satisfactory as generic distinctions. They could be used to establish sections of the genus.

A more distinct division of *Thelypteris* is that of *T. ornata*, *T. brunnea* and their allies. These are all exindusiate, mostly large ferns, with long-creeping rhizome. Their spores are perhaps also distinctive (good material not seen). I suggest that they may represent a group of independent evolution, and that perhaps they never had indusia. Generic rank for them might be considered. As above noted, *T. ornata* appears to retain a primitive frond-form.

It is remarkable that *Thelypteris* (sens. strict.) is mainly distributed (as regards Asiatic species at least) on the borders of the tropics; in Malaysia the species are mostly on the mountains, few in the lowlands, and the total number of species is smaller than in regions farther north. *Cyclosorus*, on the other hand, is preponderantly tropical, and there are many common lowland species in Malaya. That is, it looks as if *Thelypteris* had its origin on the borders of the tropics (where *T. ornata* occurs) and that the later-evolved (on several lines) species with anastomosing veins (*Cyclosorus*) became more fully adapted to tropical conditions. This however is no more than a suggestion; investigation of tropical American species, with such ideas in mind, needs to be undertaken before any definite statement can be made. It should be noted that some groups of closely allied species of *Cyclosorus* are pantropic in distribution.

The genus *Abacopteris*, as revived by Ching, is evidently derived from *Cyclosorus*, and seems to be a natural group, though it has become so diversified that its precise limits are not easy to establish. It needs further study, and may well merit recognition as a genus. It seems to be in active evolution.

Family DENNSTAEDTIACEAE

It is not possible to give a summary of the characters of this family, as those of the divergent subfamilies are so varied. All that can be said is that in the case of all subfamilies there is evidence, more or less clear, of evolution from ferns of the same stock as *Dennstaedtia* and *Culcita*. Those subfamilies which are most nearly related to *Dennstaedtia* have already been much studied, and the evidence of their relationship, as put forward by Bower, is clear and undoubted. These are therefore not discussed in detail below, but only those subfamilies which are less nearly related to the original stock, or concerning which I produce new evidence which I believe indicates a different conclusion from that usually accepted. This involves the re-arrangement of some of Christensen's subfamilies (as indicated in the summary above) and a discussion of the status and limitation of some genera.

1. Dennstaedtioideae

Here are included Christensen's genera, namely *Dennstaedtia, Microlepia, Leptolepia, Oenotrichia, Saccoloma, Ormoloma, Ithycaulon, Orthiopteris, Hypolepis*; also *Culcita* (very near *Dennstaedtia* but with 2-lipped indusia and more primitive sporangia as compared with the few species of *Dennstaedtia* which have been examined in detail) and *Monachosorum*. They are the most primitive genera in the family.

They have all creeping terrestrial solenostelic rhizomes except *Ithycaulon* and *Orthiopteris*, which have erect rhizomes. *Ithycaulon* has also scales instead of hairs, but in all other respects it is hardly distinguishable from *Dennstaedtia*. These two genera indicate separate origins of erect from creeping rhizomes, a change which has evidently occurred on other lines of evolution also, probably including *Dicksonia*; but *Dicksonia* appears to me to be a dead end of evolution, which has remained at a primitive level and has not given rise to other ferns, so that it is best kept in a separate family.

Though most species of *Microlepia* are very distinct from *Dennstaedtia*, having quite superficial sori with their indusium of quite different consistence from the edge of the lamina, some species are very near *Dennstaedtia*, having sori very near the edge. I have not studied a sufficient series of species of the two genera, but Copeland suggests that there is more than one line from *Dennstaedtia* to *Microlepia*. It seems probable also that the division between *Dennstaedtia* and *Hypolepis* is not a sharp one. *H. Brooksiae* looks rather like a *Dennstaedtia* that has almost lost its indusial cup, and *H. bivalvis* v.A.v.R. belies the usual definition of *Hypolepis* by having a small inner indusial flap.

I suggest that the main lines of evolution from the primitive *Culcita-Dennstaedtia* type have been (1) by way of *Microlepia* to *Davallia* and so to *Asplenium*, and to the LOMARIOPSIS subfamily, (2) by way of *Hypolepis* to *Pteridium* and *Pteris*, (3) to the *Tectaria*, *Dryopteris* and *Athyrium* tribes. The *Lindsaya* tribe probably arose, not from a fern like *Dennstaedtia* but from a somewhat more primitive ancestor. The origin of *Nephrolepis* is less clear.

The evolutionary lines to *Davallia* and *Pteris* have been much discussed and are reasonably clear, but the idea of *Dryopteris* arising from *Dennstaedtia* is not generally accepted; the evidence for it is discussed below. Here we may note that the genus *Oenotrichia*, which has basifixed, reniform or suborbicular indusia, shows how the *Dryopteris* type of indusium can be developed from the condition of *Dennstaedtia*.

Monachosorum, placed by Copeland without comment in his Cyatheoid series, and by Christensen near *Thelypteris*, has a creeping hairy solenostelic rhizome and a frond of the general form of the *Dennstaedtia* tribe, with leaflets unequal at the base. It has also grooved costae of the *Dennstaedtia-Hypolepis* type. Its sori are naked; presumably it has lost one indusial flap. It seems to me clearly to belong to the present tribe. [See Amendment on p. 158.]

2. LINDSAYOIDEAE

GENERAL CHARACTERS

Mainly terrestrial; a few climbers or epiphytes.

Rhizome slender, covered with bristles or rather narrow castaneous scales (not peltate at the base), vascular system usually a modified protostele; *stipes* not jointed to the rhizome.

Fronds amply divided to simple, leaflets in some cases dimidiate; *veins* free in the more amply divided forms, sometimes anastomosing in the less divided; midribs of leaflets sunk, the groove running into the rachis-groove, the thickened edge of the lamina decurrent on the edge of the rachis-groove.

Sori nearly marginal, terminal on the veins, either single or those on adjacent veins joining laterally; *indusia* attached basally and opening towards the leaf-margin, their sides sometimes attached also, the margin of the frond also thin and indusium-like or like the rest of the lamina.

Spores tetrahedral or bilateral, without perispore.

The genera are: *Tapeinidium*, *Stenoloma*, *Odontosoria*, *Lindsaya*, *Isoloma*, *Schizoloma*. Three others were also included by Christensen. Of these, *Taenitis* is, in my opinion, clearly allied to *Syngramme* and is removed to Adiantaceae; *Dictyoxiphium*, as pointed out by Copeland, is related to *Tectaria*; and I believe *Diellia* belongs with *Nephrolepis*.

The most primitive member of the tribe is probably *Odontosoria* (sens. strict.), which agrees in habit with the scrambling species of *Dennstaedtia* and *Hypolepis*, but has a simpler anatomy. There is little doubt that *Odontosoria* and *Dennstaedtia* had a common ancestor at a not very remote period. The simple anatomy of *Odontosoria* is found throughout the present tribe.

Of the Asiatic genera, *Stenoloma* has the most primitive leaf-form, with often a single vein in each ultimate segment, and an approximation to dichotomous branching in the leaflets. *Lindsaya*, with its dimidiate leaflets, and mostly much smaller size, is evidently reduced and specialized from the *Stenoloma* type. *Tapeinidium* is specialized in its long narrow pinnae or pinnules and thick texture.

The generic limits of *Lindsaya*, *Schizoloma* and *Stenoloma* are not easy to define, and all might be included in one genus. A possible and apparently sharp separation of *Lindsaya* would be of frond-form. In such a species as *L. trapeziformis* the apical part of the frond bears uniform small leaflets; then the rachis bears a series of lateral branches, each like the apical part of the frond. Using the ordinary terminology in its strict sense, such *Lindsaya* fronds have (starting from the apex) first a series of small simple pinnae all nearly of a size, and then abruptly a series of long pinnate pinnae. This is very different from the arrangement in a primitive type of fern-leaf, where the pinnae gradually increase in size and complexity from the apex downwards. If we limit *Lindsaya* to ferns with simply pinnate fronds, or bipinnate fronds of the type described, we have (in Malaya at least) a distinctive genus. But this means that such species as *L. microphylla* must be removed to *Stenoloma*; and such as *L. tenera*, *L. orbiculata* to *Schizoloma*. Then the distinction between *Schizoloma* and *Stenoloma* becomes vague. The whole question certainly needs further study, based on all species of all genera.

Isoloma is a distinctive genus with many small close pinnae nearly at right angles to the rachis, not dimidiate, articulate to the rachis, and rather coriaceous in texture, the veins all free or nearly so. The Malay Peninsula species inhabit moist shady forest, where their rather thick articulate pinnae seem incongruous.

3. DAVALLIOIDEAE

GENERAL CHARACTERS

Mostly epiphytes.

Rhizome creeping, fleshy, scaly, the scales in most cases with a peltate base; vascular system of rhizome as seen in transverse section consisting of broad dorsal and ventral steles with a variable number of intermediate small strands on either side.

Stipes in two ranks, articulated at the base, with several separate vascular strands (except *Leucostegia*).

Fronds in most species amply dissected, in a few pinnate or simple, often broadly deltoid, ultimate leaflets usually unequal at the base; *veins* free; midrib of leaflets raised, edge of lamina decurrent on to the edge of the winged pinna-rachis.

Sori terminal on the veins, close to the margin, always single (never joined laterally), with indusium attached at the base and often also along the sides.

Spores bilateral, without perispore (always?).

GENERA: *Davallia* (including *Scyphularia*, *Parasorus* and *Trogostolon*), *Humata*, *Araiostegia* (omitted by C.Chr.), *Davallodes*, *Leucostegia*, *Rumohra* (sens. strict., not of Ching). *Nephrolepis*, *Arthropteris* and *Psammisorus* are excluded and placed in Oleandroideae.

All genera except *Leucostegia* are closely related, and their limits are not always clear. *Davallodes* and *Araiostegia* at least should be united, and it might be best to include all in *Davallia*. Certainly a distinction of genera on soral characters alone is quite impossible, as indicated by the vegetatively very uniform genus *Davallodes*, which has indusia either only basally attached or attached on the sides also. A distinction on rhizome-scales alone is also not practicable. The discussion below relates to *Davallia* and its immediate allies; at the end the peculiar genus *Leucostegia* is dealt with.

SCALES. In almost all cases the scales are rather broadly peltate at the base, but (as pointed out by Arbelaez), those of *D. divaricata* are not quite peltate, but attached along a short transverse line, and cordate, possibly indicating the way in which the peltate character has arisen (see *Leucostegia* below). There is much evidence to indicate that scales have developed from hairs on many lines of evolution among ferns; and peltate scales have originated independently in Gleicheniaceae, Polypodiaceae, and *Nephrolepis* at least. As nearly all primitive ferns have a covering of hairs, it is almost certain in any case that the scales of *Davallia* were derived from hairs; yet Copeland (1929, p. 96) objects to the derivation of *Davallia* from *Dennstaedtia* (and *Microlepia*) partly on account of the scales of *Davallia*, though he has no such objection to the derivation of *Nephrolepis* and *Pteris* from hairy ancestors. The *Lindsaya* tribe show all stages in the evolution of scales from hairs, and *Leucostegia* perhaps represents a transition from the *Lindsaya* scale to the *Davallia* scale.

VASCULAR STRUCTURE. The rhizome of *Davallia* contains a complex vascular system, but it is derivable from a solenostele, by the development of perforations. *Leucostegia* shows an interesting intermediate type. The structure of *Davallia* differs from that in Polypodiaceae (also dorsiventral with 2-ranked fronds and probably derived from a primitive solenostele) in the presence of the broad dorsal and ventral steles, the latter alone producing roots. This arrangement has resemblance to the Lomariopsis subfamily of acrostichoid genera.

The stipe of *Davallia* has several vascular bundles, arranged in the usual U-shaped series in transverse section. An interesting feature is that towards the top of the stipe the two largest bundles (at the open end of the U) join together to form an X-shaped bundle, exactly as in *Asplenium*. This is evidence of the relationship of *Davallia* with *Asplenium*.

The smaller ferns of the *Davallia* group (*Humata*, etc.) have similar anatomy to *Davallia*, but reduced in complexity in accordance with their small size.

Rachis structure. All main veins of leaflets are raised and rounded on the upper surface, and at the base of each leaflet the margins of the lamina are decurrent as a narrow wing on either side of this raised main vein; the wing is continued on all the smaller rachises and sometimes on the main rachis also. As pointed out elsewhere, this is quite different from the rachis-structure of *Pteris* and *Dryopteris*, but similar to that of *Asplenium* and also to the *Lomariopsis* subfamily and to *Pteridrys*. Though less complex than the distinctive rachis-structure of *Pteris* and other genera, I believe it may be a valuable indication of relationship among groups where other characters are subject to evolutionary change. A similar structure occurs in some species of *Microlepia*, though in most the lamina is thin and so the resemblance is not marked.

Sori. It is generally agreed (except apparently by Copeland) that the sori of *Davallia* are of marginal origin, but that they have come to be superficial on the lower surface owing to unequal evolutionary development of the two indusial flaps of the ancestral Dicksonioid type. The *Davallia* indusium represents one flap, the other flap having merged with the lamina of the frond. The way in which such a change can take place may be seen in the genera *Dennstaedtia* and *Microlepia*, especially in those species of the latter with an almost marginal sorus (e.g. *M. todayensis*). In *Dennstaedtia* the sorus is enclosed in a cup, by fusion of the two flaps of the more primitive *Culcita* type; in *Microlepia* half the cup has slipped to a position of varied distance from the edge, remaining attached to the frond by both base and sides, to form a pouch. This is exactly the same type of indusium which we find in *Davallia*. Having regard also to frond-form, so closely similar in the two genera, it seems to me in the highest degree probable that *Davallia* was derived from *Microlepia*.

If we assume the *Microlepia* type of indusium to be primitive, then *Davallia* itself has departed little from it, only in some cases exaggerating the depth of the pouch (*D. solida*, etc.). The other genera however show modifications. In *Humata* the indusium is attached by the base only, its shape being semicircular to almost circular. *Humata* is certainly more specialized than *Davallia* in the small size of its fronds. *Araiostegia hymenophylloides* has indusia very much like those of the small species of *Humata*, but combined with a primitive, large and finely dissected frond-form.

The transition of the *Davallia* sorus-form to that of *Asplenium* is seen in the genus *Loxoscaphe*. This is dealt with under *Asplenium*, as evidence of the derivation of *Asplenium* from *Davallia*.

Leucostegia. This genus was established by Presl on the species *L. immersa*, and to this Beddome and other authors added other ferns of *Davallia*-like appearance, creeping scaly rhizomes, fronds of thin texture and indusia joined at the base. But these other ferns (now called *Araiostegia*) differ from *Leucostegia immersa* in various characters mentioned below, and surely are not very nearly related to it; whereas a second species, hardly different from *L. immersa* in all characters but the indusium, was placed in the genus *Davallia*. This second species (*Leucostegia pallida*) was united to *L. immersa* by Copeland in 1927, but he did not point out all the peculiarities of the genus, nor realize how different it is from *Davallia*.

The rhizome is terrestrial, and covered both with hairs (absent in *Davallia*) and shining scales; also it bears roots all over its surface, whereas they are on the ventral side only in *Davallia*. The scales are not peltate, but have bases attached to the rhizome along curved lines (ends of the lines decurrent) which leave a pattern when the scales are removed. This is much as in *Lindsaya*, but more highly developed, as the scales are wider. If the curved base were extended to a circle, and the circle reduced, we might have the peltate *Davallia* type of scale. *Leucostegia* scales differ from *Davallia* also in having small papillae on the marginal cells, at right angles to the edge, often more than one to a single cell.

The vascular system of the rhizome consists of two meristeles, arranged as if a solenostele had been slit longitudinally along each side, nearer the dorsal than the ventral surface of the rhizome. The leaf-traces are provided by a strand from each stele; root-traces arise on the outer surface of both steles. The two strands of the stipe join upwards in the same way as the two largest strands in the *Davallia* stipe, and exactly also as in *Asplenium*.

The main veins of the leaflets are grooved, not raised as in *Davallia*, and the basiscopic edge of the lamina is thickened exactly as in *Lindsaya*. In fact, *Leucostegia* is in some ways rather intermediate between *Lindsaya* and *Davallia*. I think however that *Leucostegia* represents a branch of the *Davallia* group which has preserved some primitive features, by reason of which it is nearer to the common ancestor of *Davallia* and *Lindsaya*. It is curious that what must be an old genus should still consist of only two species, and also that its distribution should be over such a wide area: from southern India to the New Hebrides.

Rumohra, confined to the species *R. adiantiforme* (not including *Polystichopsis* as proposed by Ching in 1934) is vegetatively extremely close to *Davallia*, but differs strikingly in the peltate indusia of its sori. I suggest that it is a direct derivative from *Davallia*, on a line of evolution parallel to that of *Polystichum*, which it resembles in sori and texture of fronds, but from which it differs very strongly in its dorsiventral creeping rhizome and in the costae being raised, not grooved.

4. Oleandroideae

Genera: *Nephrolepis, Oleandra, Arthropteris, Psammisorus, Diellia.*

These genera are so different that a general description of the characters of the tribe is impossible. Christensen put *Oleandra* in a subfamily of its own, and *Nephrolepis, Arthropteris* and *Psammisorus* with some doubt into the *Davallia* tribe, to which I do not think they can be at all closely allied. Copeland places *Nephrolepis* immediately after *Cystodium*, from which he believes it derived; and *Arthropteris* in his *Oleandra* series, which also includes *Davallia*.

Nephrolepis has a short erect dictyostelic stem bearing a rosette of fronds, and from this numerous slender horizontal runners, which have at first protostelic structure, developing to a dictyostele when they bear new erect leafy stems. The scales are peltate at the base, not greatly different from those of *Davallia*. The fronds are simply pinnate, with articulate pinnae, sori terminal on the veins and near the margin, indusia reniform to semicircular, or fused laterally as in *Lindsaya*. Certain cultivated varieties bear bipinnate or tripinnate fronds which may in some measure indicate the primitive leaf-form.

Oleandra has erect and branching stems, bearing articulated fronds in close groups, or creeping stems also with fronds in groups; the stems are dictyostelic and scales peltate at the base. The fronds are simple, with free veins, and a single row of sori, quite like those of *Nephrolepis*, but close to each side of the midrib, the sori not terminal on the veins.

Arthropteris and Psammisorus have slender creeping rhizomes, solenostelic, scaly, bearing articulated fronds in two ranks. *Arthropteris* has pinnae much like *Nephrolepis*, with terminal sori, indusiate or naked, indusia reniform. *Psammisorus* has anastomosing veins, the sori on these, not terminal, and exindusiate. *Diellia* has anastomosing veins and indusiate sori; in sori and frond-form it is much like *Nephrolepis*. It needs further investigation.

The habit of *Nephrolepis* reminds one forcibly of certain primitive ferns with erect stocks which are believed to have evolved from creeping ancestors, namely, *Thyrsopteris* and *Lophosoria*. These have slender runners, essentially like those of *Nephrolepis*; they appear to represent a sort of transition condition between creeping and erect habits of growth. Copeland suggests that *Nephrolepis* was derived from *Cystodium*; this is possible, but I prefer the alternative suggestion given below. *Cystodium* is nearly related to *Dicksonia* and *Thyrsopteris*; and though it does not itself produce runners, *Thyrsopteris* does so, and the possibility of such production evidently exists in this ancestral stock. It may therefore be that *Nephrolepis* arose from a Dicksonioid ancestor, near *Cystodium*, which had the runner-producing character. This ancestor must have been bipinnate, and the simply pinnate *Nephrolepis* fronds are a reduced state. The bipinnate-tripinnate fronds of cultivated *Nephrolepis* are a reasonable indication of a bipinnate ancestral condition.

As noted by Christ, and repeated by Bower (*The Ferns*, vol. 3, pp. 20–2), the soral form of *Nephrolepis* is varied. We may take as primitive those species with sori on marginal lobes, the indusia approximating in size to the lobes; these sori are not far removed from the Dicksonioid state in shape, though they are mixed and the sporangia of a more advanced type. The sori with reniform indusia, found on the commoner species of *Nephrolepis*, may then be taken as a later stage of development.

A somewhat different origin for *Nephrolepis*, and one that would link it with *Arthropteris*, is suggested by the fern called *Microlepia Hookeriana*. This has a solenostelic hairy rhizome like *Microlepia* but fronds (with articulate pinnae) of the shape of *Nephrolepis*, the sori placed on marginal lobes as in *N. acuminata* but the indusia pouch-shaped as in *Microlepia*. If we may accept *M. Hookeriana* as an ancestral form of *Nephrolepis*, we must assume that *Nephrolepis* developed for itself independently its erect leaf-bearing stems and the runner-producing habit. This is of course possible; such a development has certainly occurred on several different lines of fern evolution. And at the same time *Microlepia Hookeriana* could give rise to *Arthropteris*, retaining its creeping solenostelic rhizome but developing articulations at the base of the stipes. On this assumed origin for *Nephrolepis*, the primitive ancestor must have had a creeping solenostelic rhizome, with bipinnate fronds—something in fact very like *Microlepia*, not like *Cystodium* which has a short rather thick decumbent rootstock of radial structure, rather like that of *Cibotium*.

OLEANDRA is a very peculiar genus, and nobody has made a generally acceptable suggestion as to its origin and relationships. Copeland places it at the head of his *Davallia* series (which he says has nothing to do with *Dennstaedtia*) but has no suggestion as to its origin. It appears to me however that *Oleandra*, with its rather small simple fronds, must be a reduced type, not a primitive one which has given rise to larger ferns such as *Davallia*; and I suggest that the primitive genus most likely as an ancestor for *Oleandra* is *Nephrolepis*. The scales and sori of *Oleandra* are quite like those of *Nephrolepis*. The great difficulty as regards sori is their position near the base of the veins, close to the costa, in *Oleandra*, and their terminal position in *Nephrolepis*; but in the reduction from pinnate to simple leaf-form such a change might have taken place. The same (or nearly the same) difficulty would arise in deriving *Oleandra* from any other fern genus in the family here called Dennstaedtiaceae; and it can hardly have arisen from any in Thelypteridaceae, certainly not from Polypodiaceae.

As regards habit of growth, *Nephrolepis* and *Oleandra* seem very different; but if the erect stock of *Nephrolepis*, having produced a group of fronds close together, were to grow vertically for about 20 cm., possibly branching but not producing fronds, and then produce another group of fronds, we should have the habit of *Oleandra neriiformis* (or

O. pistillaris). Some other species of *Oleandra* have a creeping rhizome, but the fronds similarly grouped; except that in *O. Wallichii* it seems as if the continued leafless rhizome-growth after the groups of fronds is not terminal but lateral, a condition (if correct) easily derived from a runner of *Nephrolepis*. The leaves of the sporeling of *Oleandra* might possibly throw some light on the question. I do not think they have ever been described; I have never seen young plants, and they are probably not easy to find, nor the spores to grow under lowland conditions in Malaya.

5. PTERIDOIDEAE

GENERA: *Pteridium*, *Paesia*, *Lonchitis*, *Anisosorus*, *Histiopteris*; *Pteris* and *Anopteris*, etc. (as listed by Christensen); *Neurocallis*, *Acrostichum* and *Stenochlaena*.

This tribe has been so fully dealt with by Bower (*The Ferns*, vol. 3, ch. XXXVIII) that little further comment is needed here. One point however has not been mentioned, namely the deeply grooved costae with basiscopic edge decurrent on the edge of the rachis-groove (as seen in *Hypolepis* and some species of *Dennstaedtia*, also in *Dryopteris* and *Athyrium*). The sides of the groove of the costa are interrupted at the costules, and there in some species prolonged into spines; an exactly similar condition occurs in *Athyrium nigripes* and its allies.

The only genus added by Christensen to Bower's list is *Stenochlaena* (sens. strict.). This has many points in common with *Acrostichum*; its complex vascular system, pinnate fronds with glands at the bases of the pinnae and separately on the stipe, costal areoles, and translucent spores lacking perispore. *Stenochlaena* differs from *Acrostichum* in its long-climbing rhizome (a development which is quite possible from an erect stock, for the rhizome of *Stenochlaena* is radial in structure, not dorsiventral, and quite as complex as *Acrostichum*), less reticulate venation (a trivial difference), lack of capitate paraphyses and bilateral, not tetrahedral, spores. There are other cases however in which allied genera have spores differently shaped in this way.

6. ASPLENIOIDEAE

GENERAL CHARACTERS

Rhizome in a minority creeping or climbing and dorsiventral, usually suberect or erect and radial in structure; vascular system dictyostelic; *scales* peltate at the base, clathrate or nearly so.

Stipes containing two vascular strands at the base, joining upwards to form a single strand with 4 arms (more or less X-shaped).

Fronds amply dissected to simple, rarely dimorphous; *veins* free except in a few of the less dissected forms.

Sori linear along one side of a vein, in nearly all cases with a narrow indusium opening towards the costa of the leaflet which carries it, or in a lobed leaflet towards the costule of the lobe, or in some simply pinnate or simple fronds a less regular arrangement, sometimes a sorus on both sides of a vein.

Spores bilateral, with perispore.

GENERA: *Asplenium*, *Phyllitis*, *Diplora*, *Camptosorus*, *Ceterach*, *Pleurosorus*, *Pleurosoriopsis* (the last two need investigation).

ASPLENIUM AND ATHYRIUM*

ASPLENIUM has always been associated with *Athyrium*, because of their similar sori. I believe however that this is a case of convergent evolution from quite different sources, and therefore exclude *Athyrium* from the present tribe, placing it near *Dryopteris*. But because the two have been so constantly associated, and often indeed confused, a comparative account of the two at this point seems the most convenient way of demonstrating their differences and the view I take of their origin. As an example of the confusion which still occurs, it is notable that Bower uses a species of *Athyrium* (*A. lanceum* (Thunb.) Milde) to illustrate the evolution of the sorus of *Asplenium* (*The Ferns*, vol. 3, p. 142, fig. 672).

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* Including *Diplazium*.

The thesis here proposed is that *Asplenium* is derived from something like *Davallia*, and that *Athyrium* is derived from something near *Dryopteris*. This difference of origin is indicated by (1) anatomy of upper part of stipe and rachis, (2) external structure of smaller rachises of bipinnate species in their relation to leaflets, (3) vascular supply to sori, (4) rhizome-scales, (5) preponderant epiphytic character of *Asplenium*, terrestrial of *Athyrium* species. In all these characters, so far as I have observed, the two genera differ constantly. A few notes on each follow.

STIPE AND RACHIS. As observed by many authors, two vascular strands enter the base of the stipe of both genera. In *Athyrium* the two join to form a single strand of approximate U-shape in transverse section; in *Asplenium* the single strand has four ends as seen in section. Mme Tardieu-Blot has published drawings of a considerable series of examples of both kinds (*Aspl. du Tonkin*). A fusion of the two main vascular strands near the top of the stipe occurs in *Davallia* in exactly the same way as the fusion of the two sole strands of *Asplenium*.

PINNA-RACHIS AND LEAFLETS. In *Asplenium* the basiscopic edge of a leaflet is decurrent on the raised edge of the pinna-rachis. In bipinnatifid or bipinnate species the basiscopic margin of a lobe is sometimes similarly continued as a ridge across the lamina and decurrent as a ridge beside the midrib of the pinna. In *Athyrium* the raised margins of the midribs of leaflets are decurrent on the raised margins of the rachis, the edge of the lamina being decurrent on the side of the rachis, often forming a wing there, at least in the apical part of a pinna or frond. At the junction of rachis with leaflet, the edge of the rachis-groove is enlarged. In these characters, *Athyrium* agrees with *Dryopteris* *Asplenium* with *Davallia*.

VASCULAR SUPPLY TO SORI. Roth, in 1799, stated that *Athyrium filix-foemina* had a special vascular supply to the receptacle, lacking in *Asplenium*. Bower mentions this (*The Ferns*, vol. 3, p. 144) but does not indicate that he or anyone else has confirmed it He states that such a vascular supply is characteristic of the evolutionary line which he considers has led to *Dryopteris* and its allies. He does not however consider a distinct origin for *Asplenium* on that account. This question of vascular supply to the sorus needs fresh investigation. I only find the normal vein along the sorus of some *Diplazia*.

RHIZOME-SCALES. As pointed out by Milde and others, the latticed (clathrate) rhizome-scales usual in *Asplenium* are quite different from the opaque non-latticed scales of *Athyrium*. The latter agree with *Dryopteris*.

TERRESTRIAL AND EPIPHYTIC HABIT. This is not a sharp distinction, but is a very general one, and is probably significant. Here again *Asplenium* agrees with *Davallia*, *Athyrium* with *Dryopteris*. The stout roots of many species of *Athyrium* are also very different from those of any *Asplenium*.

We thus see that, on all five counts, *Asplenium* shows resemblances to *Davallia* *Athyrium* to *Dryopteris*. The latter resemblance has been remarked upon by Christensen and others (Ching has erroneously stated that *Thelypteris* and *Athyrium* are nearly allied), but no close relationship between *Asplenium* and *Davallia* seems to have been suggested. There is however a significant group of species showing intermediate characters, now usually placed in a section *Loxoscaphe* of *Asplenium* but included in *Davallia* by Hooker *A. theciferum* has an erect stock, with vascular anatomy of *Asplenium*, but sori nearly like *Davallia*, showing also various stages of transition from a terminal *Davallia*-like position of the veins to a lateral one, in which the receptacle becomes somewhat elongated along the vein. The sorus is then very like that of *Asplenium Belangeri*.

The origin of *Asplenium* from ancestors with large finely-dissected fronds, and sori like those of *Loxoscaphe*, seems quite possible. Such a primitive *Asplenium* must have had a creeping dorsiventral rhizome; but this can hardly have had so complex a vascular structure as that of *Davallia*. Probably *Davallia* and *Asplenium* diverged from a common source, *Davallia* to its long-creeping epiphytic rhizome with complex anatomy and *Asplenium* to an erect stock with radial symmetry (usually also epiphytic), some species still retaining a dorsiventral structure (groups of *A. unilaterale* and *A. scandens*). The curious method of fusion of the vascular bundles in the upper part of the stipe must have been a character of the *Davallia-Asplenium* ancestor; this character is found also in the somewhat primitive *Leucostegia*, in *Diellia* and other *Davallia*-allies. *Davallia* retains it, though developing a series of separate smaller vascular strands in addition to the two main ones.

EVOLUTION OF SORAL FORM IN ASPLENIUM AND ATHYRIUM. If we postulate an origin of *Asplenium* from the *Davallia* group of genera, and of *Athyrium* from the *Dryopteris* group (or from its immediate ancestors) we can trace from these different origins the evolution of the linear soral shape which is common to the two genera.

For *Asplenium*, the early stages of change from a *Davallia*-sorus to a linear sorus are figured by Arbelaez (*Bot. Abh. Goebel*, no. 14, p. 91, fig. 35, 1928). These stages show first a cup-shaped sorus terminal on a short vein, and then this vein shortening until the sorus becomes sessile on the side of the next larger vein, along which its receptacle finally spreads. We have only to extend the spreading of the receptacle to produce a typical elongate *Asplenium* sorus. From such an origin, the sorus is produced *on one side of the vein only*; this is the primitive *Asplenium* condition. But sometimes *Asplenium* species have sori on both sides of a vein. This is a secondary development, dealt with below.

For *Athyrium*, we postulate an origin from a sorus with reniform indusium, probably not terminal on a vein, such as occurs in *Dryopteris*. In such a sorus, the receptacle is horseshoe-shaped (Bower, *The Ferns*, vol. 3, p. 124), extending for a little distance on both sides of the vein and crossing the vein at the apex of the sorus; the indusium is attached on the crest of the vein-ridge. We have only to extend such a sorus along the vein to produce a condition found in some species of *Athyrium*; and a still commoner condition is produced by unequal extension of the receptacle on the two sides of the vein, giving a **J**-shaped sorus. The next stage is for the receptacle and indusium to be interrupted at the distal end of the sorus, the result being a receptacle with indusium separately on each side of the vein. This is the condition of species placed in the genus *Diplazium*, but it is not sharply distinct; both forms of sori can be found on the same frond in some species of *Athyrium*, e.g. *A. lanceum* (Thunb.) Milde, as figured by Bower. Finally, a one-sided sorus can develop from a **J**-shaped sorus by abortion of the shorter limb of the **J**. Thus *the single-sided sorus*, which is primitive in *Asplenium*, *is derivative in Athyrium*.

In *Athyrium filix-foemina*, which is probably a primitive type of *Athyrium* (it has highly dissected fronds) there are almost reniform indusia, **J**-shaped indusia and one-sided indusia, all on the same leaflet. The sori nearest to the reniform shape are always on the basal acroscopic vein of a leaflet or lobe; the higher veins commonly bear one-sided sori facing the midrib. Similarly, in less primitive species of *Athyrium*, with longer sori, the basal acroscopic sorus is double (Diplazioid), though the receptacle and indusium do not cross the vein, whereas the sori on the other veins are mostly single. This explains the origin of the double sorus on the basal acroscopic vein in most species of *Athyrium*, and the fact that the upper sori of *Athyrium* face the midrib of their lobe or leaflet.

Thus in *Asplenium* and *Athyrium* we have single-sided sori which face the midrib of their leaflet. But towards the apex of an *Asplenium*-pinna the leaflets grade into lobes, and these lobes grade into teeth on the edge of an apical lamina; the sori on this apical lamina face the midrib of the pinna. There is thus a transition region in which the change occurs from sori facing the midrib of a lobe to sori facing the pinna-midrib. At this transition-region we sometimes have veins with sori on both sides, usually basal acroscopic veins (these being nearest the pinna-midrib), especially in species which show much condensation of the lamina.

Thus both *Athyrium* and *Asplenium* have produced double sori on the basal acroscopic veins of some lobes, but the two kinds of double sori are quite different in origin; and whereas the double sorus in this position is primitive and common in *Athyrium* (often found on all lobes of a pinna), in *Asplenium* it is derivative, less common, and not usually found on all lobes.

EVOLUTIONARY TRENDS WITHIN AND FROM ASPLENIUM

A study of the spores of Malaysian and other Asiatic *Asplenia* in the Singapore herbarium has shown the possibility of grouping them according to spore characters, and that this grouping also corresponds in the main with vegetative form. This grouping appears to show several evolutionary trends within the genus, one of them leading to the genus *Diplora* (which has simple fronds). The other small genera of this tribe can probably be similarly traced to other groups in *Asplenium*; I have not the material available to deal with them, but it seems likely that *Diplora* and *Phyllitis*, with similar frond-form and soral characters, are cases of convergent evolution from different groups in *Asplenium*. The following is a summary of the sections into which I have divided the Malaysian species which I have examined.

(1) *Asplenium scandens group*. Rhizome long-creeping or climbing; fronds relatively narrow, finely dissected (*A. scandens*) to simply pinnate (*A. borneense*) or simple (*A. scolopendroides*, *A. batuense*, *Diplora D'Urvillaei*, *A. epiphyticum*). Spores pale, translucent, median wing of perispore produced into numerous hair- or spine-like points which may equal in length the width of the spore, other such points from the face of the spore, 15–20 in all.

The long-creeping or climbing rhizome is characteristic. It is not dorsiventral in *A. epiphyticum*; the other species need studying. There is every indication that *A. scandens*, with long-creeping rhizome and highly dissected fronds, is a primitive form, though it does not appear to have given rise to the main bulk of the genus.

A. scolopendroides and *A. epiphyticum* both have deeply dissected fronds on young plants, simple entire fronds on old plants, the young plants thus preserving primitive characters. *A. scolopendroides* has also a raised line marking the position of the edge of the indusium in the young frond; such a raised line is also found between the facing pairs of indusia in *Diplora*, and occasionally similar facing pairs of sori are found in *Asplenium scolopendroides* (also in *A. batuense*, but without the raised line). It is evident that these ferns were all derived from ancestors with highly dissected fronds, and that in condensation the arrangement of sori on adjacent veins facing each other is possible. Such an arrangement occurs as a regular feature in *Diplora*, as an exceptional one in *Asplenium scolopendroides*; both probably from the same common parent, as indicated by their similar habit and spores. Young plants of *Diplora* should be examined. *D. longifolia* has spores with a smooth, not spiny wing; it is apparently an exceptional species which has lost the common spore-character. It indicates that spore-characters alone may not be a safe guide, but combined with other characters they may be very useful.

(2) *Asplenium unilaterale group*. Rhizome short-creeping, dorsiventral, plants rather small, apparently mostly simply pinnate, the lower sides of the pinnae much cut away. Spores dark, with wide thin transparent median wing to the perispore, its edges irregular and often toothed, folds of the perispore anastomosing over the spore-surface to a moderate or elaborate extent. Species: *A. unilaterale* and near allies, *A. normale*, *A. cheilosorum*. Mme Tardieu-Blot has excellent diagrams of the rhizomes of some of these ferns, showing their dorsiventral structure. They are mostly rock-plants, or streamside plants.

Though reduced in size, these species retain the primitive creeping rhizome. The same frond-form (pinnae cut away on the basiscopic side) is shown by *A. tenuifolium*, but amply dissected, probably showing the ancestral condition of *A. unilaterale*; but *A. tenuifolium* has developed an erect rhizome. *A. loxocarpum* Copel. from Sumatra and *A. Wrightii* from China have the spores of the *A. unilaterale* group but fronds near those of *A. tenerum* (group 3). They are an indication of inter-relationships between the two groups. The ferns of group 2 have retained the primitive rhizome-characters, lost by group 3, which however in some cases preserves a more primitive frond-form.

(3) *A. tenerum group.* Epiphytic or rock-plants (sometimes terrestrial), with more or less massive erect stock and a rosette of fronds, forming a basket (in *A. tenerum* functioning as a leaf-collecting nest, as in *A. nidus*); fronds finely dissected (*A. bulbiferum*) to simply pinnate (*A. tenerum*, *A. salignum*) to simple (*A. squamulatum*, probably also *A. nidus*); fronds pale green, indusia wide and pale; edges of lamina usually with regular rounded teeth; costae raised, without a ridge on each side, on the upper surface. Spores pale but more or less opaque, granular, median wing minutely toothed with thickened edge, moderately wide, the folds across the face of the spore moderately anastomosing.

This is one of the main groups of the genus; its primitive species have quite large and much-dissected fronds, with a single vein to each lobe of each leaflet. They are not far removed from the *Loxoscaphe* group which are mentioned above as indicating the transition from *Davallia*- to *Asplenium*-sori. This group evidently changed from creeping to erect rhizome at an early stage, whereas the *A. scandens* group retained the creeping type. *A. nidus* has exactly the habit of this group of species, and fairly similar spores, but its venation is specialized, and it is far larger than most members of the group. I think, however, that it probably belongs here.

(4) *A. robustum group.* Rather large species, mainly epiphytes, with highly dissected rather coriaceous fronds; rhizome not dorsiventral, but not massive and erect as in the *A. tenerum* group; pinna-rachis with raised edges upon which the basiscopic margin of each pinnule is decurrent; midribs of unlobed leaflets raised, but deeply lobed leaflets (or lobed apex of a pinna) with a small ridge on each side of the midrib, like the raised edge of the rachis, these ridges being the decurrent bases of the basiscopic sides of the lobes, indicating condensation of the lamina from a more dissected condition. Spores pale, translucent, with rather broad almost entire median wing, with few other folds of the perispore.

This group has fronds almost as large and finely dissected as any in group 3, but it is clearly quite distinct in texture, as well as in the indications of condensation in the larger leaflets (no such condition occurs in group 3). Probably the two groups diverged at an early stage in the evolution of the genus. Ferns of the *A. robustum* group do not have the nest-habit of *A. tenerum*; they often grow in association with *A. nidus*, taking advantage of its humus-collecting.

(5) *A. caudatum group.* Closely related to group 4, but the fronds less divided, usually pinnate with deeply lobed to almost entire pinnae, some of which show the same condensation indications as described for *A. robustum*. In *A. macrophyllum*, which has nearly entire pinnae, the pinna-midrib has raised edges, and is quite different from the midrib of a pinna in the *tenerum* group. Spores dark, more or less translucent, median wing of perispore entire, narrow to moderate in width, folds across face of perispore moderately anastomosing.

7. BLECHNOIDEAE

GENERAL CHARACTERS

Terrestrial ferns with stout erect rhizome.

Fronds pinnate or bipinnate; *veins* free or with some anastomosis.

Sori short or long, on veins or vascular commissures parallel to the midrib of a pinna, in a single line or (in *Doodia*) in 1–3 rows on each side, protected by a marginal indusium (if the fertile pinna is narrow) or a superficial, intramarginal to subcostal exterior and introrse membranous indusium.

Spores bilateral, with or without perispore.

GENERA: *Blechnum*, *Sadleria*, *Woodwardia*, *Doodia*, *Brainea*.

Bower has proposed the theory that *Blechnum* and its allies have originated from the family Cyatheaceae by way of a reduced ancestor, such as *Matteuccia intermedia*, with narrow fertile pinnae. This involves the assumption that *Lomaria* is the primitive group in

Blechnum. This in turn involves the difficulty of the origin of *Eu-Blechnum*, with its uniform sterile and fertile fronds, from *Lomaria*. Bower proposed his theory of the flange to solve this difficulty; this makes the blade of the fertile *Blechnum* leaf an organ of different origin from the identical sterile blade. Both Copeland and Christensen have objected to this theory, and I agree with them. Bower himself admits that the facts would permit a contrary reading of the series of changes, so that *Eu-Blechnum* could be regarded as the primitive condition and *Lomaria* as derivative, 'but this view would present comparative difficulties in relation to the sorus and the indusial flap, while it would conflict with physiological probability' (*The Ferns*, vol. 3, p. 173). Certainly this view would exclude an origin from *Matteuccia*; but other origins are possible, and (I suggest) more likely. And to state that *Eu-Blechnum* being primitive conflicts with physiological probability goes in the face of all the facts. Some of the species of *Eu-Blechnum* are among the commonest tropical ferns, of very wide distribution and obviously most successful. Why should they not represent the primitive form of the genus? Such a view would postulate a tropical origin for *Blechnum* (the majority of ferns are tropical) and the derivation from it of specialized types adapted to cooler and more seasonal climates (tropical species of *Lomaria* are mostly mountain plants). This seems to me a reasonable view.

We then have to find another origin for *Eu-Blechnum*. Bower himself provides one, if we read in the reverse sense his statements about the breaking-up of the fusion-sorus of *Blechnum puncticulatum* var. *Krebsii* (*The Ferns*, vol. 3, pp. 185–8). Why should not these abnormal archings of the sorus between the veins, and breaks in the sorus, indicate how the fusion-sorus was derived by joining of Asplenioid sori? This seems to me a far more likely state of affairs than the contrary. It is very easy to derive the condition of *Blechnum* or *Doodia* from the soral arrangement of *Asplenium caudatum*, where the sori are on veins close to and nearly parallel with the midrib of the pinna, and face it. An origin from *Phyllitis* seems less likely, as this would involve the reversion to a pinnate frond from the simple-frond state; but possibly a pre-*Phyllitis* had scolopendroid sori on pinnate fronds. In either event, an origin of *Blechnum* and its allies from an Asplenioid source is possible; and it is fairly evident that *Phyllitis* itself is derived from *Asplenium* by the retention of certain sori only when reduction of the lamina took place. (An exactly similar reduction, almost certainly on a different evolutionary line, has occurred in *Diplora*).

As regards the deeply bipinnatifid *Woodwardia*, and *Doodia*, they may have been derived from a bipinnate *Asplenium*; and the proto-Blechnoid fern may even have been bipinnate, giving rise to *Woodwardia* by the incomplete fusion of sori and to *Blechnum* by reduction to a pinnate condition.

As regards vascular anatomy, *Asplenium* is simpler than *Blechnum*, especially in the stipe, and *Blechnum* does not show the peculiar fusion of the larger adaxial bundles which occur in *Asplenium* and *Davallia*. This is evidence against an origin from *Asplenium*; and the predominant epiphytic habit of *Asplenium* (counting also rock-plants which are not truly terrestrial) is a contrast to the strictly terrestrial habit of *Blechnum*. Possibly a source of *Blechnum* might be sought in *Athyrium*, a terrestrial genus; so far as sori are concerned, *Athyrium* might equally with *Asplenium* give rise to the condition of *Blechnum*. Unfortunately the character of rachis-structure, which distinguishes clearly the more dissected species of *Athyrium* and *Asplenium*, is not clear in *Blechnum*. So far as it goes, it would indicate a relationship to *Asplenium* rather than to *Athyrium*, as there are no raised edges of the costae and no interruption of a shallow rachis-groove at junction of rachis and costa. The rather tough texture of *Blechnum*, and the fact that most species are ferns of open places rather than forest shade, is in favour of an origin from *Asplenium*.

The matter needs further investigation, especially as regards species of *Blechnum* which show a breaking of the fusion-sorus (what is their stipe-anatomy?). Provisionally, I place *Blechnum* near *Asplenium*, thus deriving it ultimately from the *Dennstaedtia* stock. There appears no definite reason for supposing an origin from Cyatheaceae.

I have investigated the soral conditions and vascular supply of the Malayan species of *Blechnum*, and add a note on them here, as they serve to illustrate a phase of evolution within the genus. The species are: *B. indicum*, *B. orientale*, *B. Finlaysonianum*, *B. vestitum*.

In *B. indicum* the sorus is seated on the outer margin of a row of distinct costal areoles; it sometimes tends to break up irregularly into short sori, a condition rarely seen in *B. orientale*. The outer veins of the areoles of *B. indicum* are clearly seen as separate from the midrib on the upper surface of a fertile pinna. This is not the case with *B. orientale*, in which the soral vein is quite distinct from the normal veins and at a different level, being supplied by numerous feeding veinlets from the normal veins. In *B. orientale* also the sorus is closer to the midrib, and the line of the soral vein is hidden by the thick-walled colourless cells of the midrib. In *B. Finlaysonianum* the soral vein is a little further from the midrib than in *B. orientale* and clear of the thick-walled cells, but it is not seen on the surface of the frond.

We may thus regard *B. indicum* as the most primitive among Malayan species of *Blechnum*. It is in fact not very far removed from the condition of *Woodwardia auriculata* Bl., where the only anastomosis is in the costal areoles, but all the sori are confined to single areoles. If we extend the sori of *W. auriculata* and transform the frond from bipinnatifid to simply pinnate, we have very much the condition of *Blechnum indicum*, even to the toothed edges of the lamina, which are not found in *B. orientale*.

We may thus regard the *B. orientale* condition as derived from the *B. indicum* condition by the development of a special vascular supply for the sorus in place of the outer veins of the areoles, and the movement of the sorus closer to the midrib. The only further specialization found in *B. Finlaysonianum* is in the great increase in thickness of the midrib on the lower surface in fertile fronds; the midrib has a wide flat outer surface and hollowed sides, so that the young sori have a completely enclosed chamber in which to develop. (This is not an adaptation to dry conditions, as *B. Finlaysonianum* is always found in forest shade, *B. orientale* in full sun.)

Another difference between *B. indicum* and *B. orientale* is in the numerous auricles all down the stipe of the latter. These auricles are found in few species of *Blechnum*; they resemble the auricles which occur in some species of *Thelypteris* and *Cyclosorus*, and, as in these genera, are evidently a special development within the genus *Blechnum*, not a primitive condition. The auricles of *Cyclosorus* and *Blechnum* all have glands at the base, which are functional in very young fronds only, but the nature of the glands is different in the two genera. *Blechnum* glands are perhaps more comparable in function with those of *Stenochlaena* and *Photinopteris*.

In *Blechnum vestitum*, our Malaysian representative of the *Lomaria* group with narrow fertile pinnae, the indusium is quite distinct from the edge of the frond-lamina (which is not the case in *Matteuccia*). The vascular supply to the sorus has become further specialized (as compared with *Blechnum orientale*) to meet the needs of a wider fertile area. The whole lower surface of the fertile frond in a broad longitudinal band has a layer of storage tracheids, which connect the widened veins of this area. The veins as seen from above are quite free and do not anastomose, the inter-connecting vascular tissue being entirely a secondary development as in *B. orientale* but much more extensive. It is thus natural to regard *B. vestitum* as a specialized derivative of the *Eu-Blechnum* stage, derived perhaps direct from a species similar to *B. indicum* with toothed pinnae and lacking auricles on the stipe. The *Lomaria* condition consists in a reduction of the lamina to a width just beyond the indusium, and a broadening of the soral area, with corresponding elaboration of the vascular supply. *Lomaria* is in fact an acrostichoid type which has managed to retain an indusium.

The *Lomaria* condition has perhaps originated, like the acrostichoid condition in other groups of ferns, on more than one evolutionary line, so that individual *Lomaria* species may be more nearly related to species in *Eu-Blechnum* than to others in *Lomaria*. A study of *Blechnum* with this idea in mind would be interesting.

The genus *Brainea*, as pointed out by Bower, is a *Blechnum* with reduced subacrostichoid fertile fronds, lacking indusia. The venation is very close to that of *Woodwardia* (making allowance for the fact that *Brainea* has simply pinnate fronds) and the fronds are very similar in aspect to *Blechnum indicum*. The stock is elongated into a short trunk, as in several species of *Blechnum*.

8. LOMARIOPSIDOIDEAE

GENERAL CHARACTERS

Rhizome creeping or climbing or epiphytic, dorsiventral, with a broad basal vascular strand which supplies the roots and one or more dorsal strands (the leaves in two or more ranks according to the number of dorsal strands); *stipes* jointed to the rhizome or more usually not, containing several separate vascular strands; *scales* peltate, small or large, those on stipe and frond smaller than on rhizome; no unicellular hairs.

Fronds simple, simply pinnate or bipinnate, the pinnae in climbing and epiphytic genera jointed to the rachis, terminal unjointed lamina present or not; distinctive *bathyphylls*, usually more dissected than the acrophylls, present in some climbing genera; *veins* free, or uniting near the margin, or in several series of areoles with or without free excurrent included veins. (See Holttum, 1932, 1938.)

Fertile fronds with reduced lamina, covered beneath with sporangia (except in Thysanosoria), a special vascular supply to the sporangia developed or not.

Spores with perispore.

GENERA: *Egenolfia*, *Bolbitis*, *Lomariopsis*, *Thysanosoria*, *Teratophyllum*, *Lomagramma*, *Elaphoglossum*.

The distinctive characters are the dorsiventral rhizome with its broad root-bearing ventral vascular strand, the acrostichoid condition, in most cases the simply pinnate fronds with free veins and the perispore.

The primitive leaf-form of the tribe is probably indicated by the bathyphylls of *Teratophyllum*, which are bipinnate. In *T. Wilkesianum* and allied species, the bathyphylls are large, and not unlike the *Davallia* tribe in aspect, except for the articulation of pinnae and pinnules. The only member of the tribe which shows any indication of separate sori, even as an abnormal condition, is *Thysanosoria*; here the sori are terminal on the veins, on small marginal lobes of the lamina. Together with the dorsiventral structure of the rhizome, and the shape of the bathyphylls of *Teratophyllum*, this is a good indication of an origin from the Dennstaedtioid ferns, probably on a line near *Davallia*, which has also a ventral root-bearing stele and peltate scales. But the *Lomariopsis* tribe do not show the joining of the large stipe-bundles as in *Davallia*. The rachis of all members of the tribe is winged, and the edge of the lamina of pinnae is decurrent on the wing (unless they are jointed) as in *Davallia*.

Christensen places these genera (except *Elaphoglossum*) under the heading 'acrostichoid genera of probably Dryopteroid origin'. But their dorsiventral rhizome is unlike that of the Dryopteroid ferns, and a direct origin from an ancestor with creeping dorsiventral rhizome is far more probable. Moreover, *Thysanosoria* gives us an indication of the terminal sori of such an ancestor. In assuming an origin of this tribe direct from a Dennstaedtioid source, somewhere near *Davallia*, we make it a parallel development to the *Dryopteris* tribe, not a derivative of the latter.

The primitive condition of the rhizome of this tribe must have been that with two-ranked fronds, a condition which has persisted in *Davallia* and in most other Dennstaedtioid ferns which retain a dorsiventral rhizome. In the *Lomariopsis* tribe, it occurs in all young plants, and in mature plants of *Eu-Teratophyllum* and *Elaphoglossum* and some species of *Bolbitis*. In old plants of the other genera, there is a widening of the rhizome to admit the extra rows of leaves, and it is usually distinctly flattened, the upper surface ribbed with the decurrent leaf-bases. In *Bolbitis* at least there are branch-buds in association with the lateral rows of leaves, in a comparable position to the branch-buds of

Dennstaedtia and *Davallia*. Bower gives a drawing of a cross section of the rhizome of *Lomariopsis sorbifolia* (he calls it *Stenochlaena*; *The Ferns*, vol. 3, p. 177, fig. 698) and states that there are roots originating in the leaf-gaps. No emergent roots ever so originate in the present tribe, and the vascular strands in question probably belong to branch-buds, which rarely develop in *Lomariopsis*.

The genera of the tribe may be divided into three groups: (1) *Egenolfia* and *Bolbitis* with short-creeping rhizomes, usually growing on rocks in shady forest, sometimes climbing short distances up tree trunks but never high-climbing; (2) *Lomariopsis*, *Thysanosoria*, *Teratophyllum*, *Lomagramma* with high-climbing rhizomes, usually starting life on rocks or the bases of trees or the forest floor, and always rooted in the ground; (3) *Elaphoglossum*, always epiphytic (at least in Malaysia; perhaps including rock-ferns in South America), with rather short, not high-climbing rhizome. The rhizome-habit thus divides the genera biologically into three distinct groups, each with a different set of environmental conditions to which it must be adapted. These conditions have doubtless been the cause of leaf-differences. The creeping rock-ferns, usually growing beside streams, have the most uniform environment, and have in most cases no articulation of pinnae or fronds. The high-climbing ferns, rooted in the earth, their fronds far from the water supply, may seasonally suffer from dry conditions, and all of them have pinnae jointed to the rachis, their fronds on the whole being fairly thin in texture (few if any grow in places exposed to the sun). *Elaphoglossum*, with simple fronds, has these jointed to the rhizome, and the fronds are usually fleshy or leathery, except in those species which only grow in moist shady places.

FRONDS. Bipinnate fronds are found in adult plants (or as acrophylls) only in *Lomagramma polyphylla*, *Teratophyllum articulatum* and *T. Wilkesianum*; otherwise such fronds are only found as bathyphylls in *Teratophyllum*. Transition-fronds between such bathyphylls and simply pinnate acrophylls also occur in various species of *Teratophyllum*. The remaining high-climbing ferns of the group have simply pinnate fronds with entire or at most slightly lobed pinnae. In *Lomariopsis* many species have quite simple entire fronds on young plants; such fronds are closely similar in form and venation to fronds of *Elaphoglossum*, and simple fertile fronds are sometimes produced by *Lomariopsis*. In all these genera the veins are free, except *Lomagramma*.

In *Bolbitis*, the pinnae are often more or less deeply lobed, and the veins anastomose. There is a gradual series of increasing complication of anastomosis, beginning with the free-veined species of *Egenolfia* (very closely allied to *Bolbitis*) and ending with such species as *B. heteroclita* and *B. diversifolia*. Young plants of *B. simplicifolia* (nearly allied to *B. heteroclita*) have pinnate leaves with free veins, indicating the ancestral state of the genus.

Copeland (1941) has objected to Ching's association of *Bolbitis* (sens. strict.) with the Asiatic ferns called by Copeland *Campium*, stating 'as to the real *Bolbitis*, I merely repeat myself, that it is derived from *Phlebodium*, and I have yet to see any refutation of the evidence by those who ignore it. Its resemblance to *Campium*, however complete, is none the less casual, the result of convergent evolution'. *Phlebodium* is a near ally of *Polypodium*. I have examined specimens of the type species and of other tropical American species of *Bolbitis* in the Kew herbarium, and find that all agree with the Asiatic species which Copeland calls *Campium* in dorsiventral rhizome, with broad root-bearing ventral stele, and in spores (which have perispore), in both these fundamental characters differing from *Phlebodium*. I see no reason whatever for generic separation of the Asiatic *Campium* from the American *Bolbitis*, and every reason to include the pantropic genus (*Bolbitis*) formed by their union in Lomariopsidoideae. The only resemblance to Polypodioid ferns is in venation, and that not in all cases. This resemblance seems to me one of convergent evolution.

In the high-climbing genera, the lateral pinnae are jointed to the rachis, and fall from old fronds. In most species of *Lomariopsis* there remains the apical lamina, in shape like a pinna, continuous with the rachis, but in *Teratophyllum* and *Lomagramma* all pinnae are jointed, except in the bathyphylls. In a few species of *Lomariopsis*, in the West Indies and Madagascar, the apical lamina is reduced to a rudiment, which is always distinctly visible. Presumably this rudiment is quite aborted in the other genera.

FERTILE FRONDS. The fertile pinnae of all genera are much narrower than the sterile and are quite covered with sporangia except in *Thysanosoria*, without any thin sterile margin such as occurs in *Stenochlaena*. In those species of *Teratophyllum* which have been investigated, there is a special vascular supply to the sporangia. The form of this varies according to the width of the fertile pinnae (see *Gard. Bull.* vol. 5, pp. 288, 296), which in most species are very narrow and fleshy, in *T. rotundifoliatum* relatively broad. There is no special vascular supply to the sori in *Lomariopsis*, but the veins of the fertile pinnae sometimes join near the margin. An exactly similar condition occurs in *Elaphoglossum*. The fertile pinnae of *Lomagramma* are usually very thin, and with a closely anastomosing venation the sori are apparently adequately supplied without further development of vascular tissue. In this matter therefore *Teratophyllum* is in advance of the other genera, though in its bathyphylls it retains a primitive character.

SPORES. The spores of all genera except *Lomagramma* (so far as investigated) have a well-developed perispore, usually consisting of a convoluted wing, varying in size. In some species of *Lomariopsis* and in some of *Elaphoglossum* (Bower, *The Ferns*, vol. 3, p. 237) the wing is modified to a large number of small flat projections, or to spines (an exactly similar development, on a quite different evolutionary line, occurs in *Thelypteris* and *Cyclosorus*). In *Lomagramma*, all species examined have very thin-walled spores, quite lacking in perispore. It is suggested that the perispore has been lost in the course of evolution. *Lomagramma* species all grow (so far as recorded) in their young stages on moist rocks beside streams, and all are ferns of shady forest. The spores may be an adaptation to such moist conditions.

ELAPHOGLOSSUM. Christensen places *Elaphoglossum* in a separate subfamily at the end of his scheme, remarking that its systematic position is doubtful. Christ, in his monograph of the genus, suggested that the only other genus to which it seemed nearly related was *Syngramma*. Bower, accepting this suggestion, adds to it the further suggestion that the primitive genus from which both are derived was *Metaxya*. Copeland (*Univ. Calif. Publ. Bot.* vol. 16, p. 103) states that he believes *Elaphoglossum*, as at present accepted, to be a mixed group, not of a single origin. He states 'the majority of the oriental species are relatives of *Cyclophorus*' but gives no indication of his reasons for this statement.

Copeland's suggestion is improbable, on account of the almost always free veins of *Elaphoglossum* and the universal complex anastomosing venation in all Polypodiaceae (including *Cyclophorus*) except the very reduced *Polypodium vulgare* and its allies. It is further improbable on account of the presence of the broad rooting ventral vascular strand in *Elaphoglossum*, not found in *Cyclophorus*; and most of all on account of the perispore on the spores of *Elaphoglossum*, such as occurs in no members of the family Polypodiaceae (as here limited).

As far as rhizome-anatomy and venation go, *Syngramma* is a more likely ancestor for *Elaphoglossum*. But *Syngramma* has very different spores (tetrahedral and smooth), and no Gymnogrammoid fern has hitherto been shown to have developed a perispore; further, in vascular structure and scales *Elaphoglossum* is much in advance of *Syngramma*. The proposition that the Malaysian and quite specialized genus *Syngramma* is an intermediary between the primitive monotypic South American *Metaxya* and the pantropic but predominantly South American *Elaphoglossum* seems extremely unlikely.

As regards an origin of *Elaphoglossum* direct from *Metaxya*, the disposition of sporangia in the latter, the shape and venation of its pinnae, and its creeping solenostelic rhizome, would present a possible basis for the necessary evolutionary changes, but the gap between the two is very wide.

I submit that a far more probable origin of *Elaphoglossum* than either of those proposed by Copeland and Bower is from *Lomariopsis*. *Elaphoglossum* agrees with *Lomariopsis* in essentials of rhizome-structure; its rhizome is more fleshy than that of *Lomariopsis* (more like *Bolbitis*) with bigger gaps between the dorsal meristele and the basal rooting one, and it has only two-ranked fronds, which however was certainly the primitive condition of *Lomariopsis*. The rhizome-scales of both genera are peltate at the base. The venation and shape of the lamina of *Elaphoglossum* are closely similar to those of the simple early fronds of *Lomariopsis* or to the terminal lamina of its pinnate fronds, except that in some species of *Elaphoglossum* the veins anastomose towards the margin. (In the derivative genus *Hymenodium* the reticulate veins are very much as in *Lomagramma*, which is closely related to *Lomariopsis*). In the fertile fronds of *Elaphoglossum* there is no additional vascular supply to the sporangia beyond the normal vein system; this is true also of *Lomariopsis*. Finally, the spores of Malaysian species of *Elaphoglossum* (*E. callifolium*, *E. decurrens*, *E. melanostictum*, *E. yunnanense*) have a perispore essentially similar to that of the Malaysian species of *Lomariopsis*; it is winged, the wing variously folded and convoluted.

The main differences of *Elaphoglossum* from *Lomariopsis* are the invariably simple and more fleshy fronds, the articulation of fronds to rhizome, and the epiphytic habit. These characters are probably all connected together. The reduction of lamina (and its thickening) is clearly an adaptation to epiphytic life, and also the articulation of the stipes. Such articulation has developed on several other distinct lines of fern evolution, so that its separate occurrence here is not improbable. And there are some species of *Eu-Teratophyllum* (*T. ludens* certainly) which have rather crudely articulated stipes. If we are right in ranking *Lomariopsis* somewhere near *Davallia*, articulation has occurred in the latter (parallel) group which has also adopted an epiphytic habit.

Lomariopsis, like *Elaphoglossum*, is pantropic, and has many species. Possibly *Elaphoglossum* may have had more than one origin from within the genus *Lomariopsis*.

9. DRYOPTERIDOIDEAE

GENERAL CHARACTERS

Terrestrial ferns with (in all except a small minority) erect or suberect *rhizomes* of radial structure with fully developed dictyostele; *stipes* with several vascular strands; *scales* without stiff unicellular hairs, marginal teeth when present formed of two adjacent cells.

Fronds amply divided with free veins (except *Cyrtomium*), leaflets with unequal base; costae of leaflets grooved, the edge of the groove decurrent on a similar interrupted groove in the pinna-rachis, edge of lamina decurrent on side of rachis.

Sori round, usually with indusium; *indusium* basally attached and round to reniform, or peltate, or in few cases globose or nearly so; *spores* bilateral, with perispore.

GENERA: *Woodsia; Stenolepia, Acrophorus, Diacalpe, Peranema, Lithostegia; Dryopteris, Polystichum, Polystichopsis* (not *Rumohra* sens. strict.), *Cyrtomium, Didymochlaena* (*Maxonia* and *Polybotrya*?); *Gymnocarpium.*

There is general agreement that these genera are allied together. Those at the beginning of the list have indusia variously shaped; the rest have reniform or peltate indusia. The former genera also have coarse multicellular hairs on the upper surface of veins and on the margins of costae, costules and rachises; similar hairs occur in *Cystopteris tenuisecta* and *Athyrium Boryanum*. *Athyrium* and *Cystopteris* are here considered as a group parallel to the present tribe, from a common ancestral stock. Presumably *Dryopteris* and the other genera lost these hairs in the course of their evolution. *Gymnocarpium* is an aberrant and doubtful member of the group; I have no good material for examination and cannot make any comment on it except that it agrees in scaliness, frond-form and the pinnule-rachis relation mentioned below. It retains a primitive, apparently dorsiventral rhizome.

Most authors have considered that the *Woodsia* and *Dryopteris* group of genera originated from Cyatheaceae. This theory has been set forth most fully by Bower, whose evidence is examined below. My contention is that this evidence is no proof of an origin from Cyatheaceae, and that an origin from *Dennstaedtia* or an allied genus is far more probable.

Bower regards *Woodsia* as a primitive Dryopteroid fern, and states that it has the following characters in common with Cyatheaceae: upright habit, chaffy scales, pinnation of the leaves, open venation, basal, sometimes continuously ring-like, indusium, signs of a gradate sequence of sporangia (*The Ferns*, vol. 3, p. 112). He further states (p. 100) that prothalli of *Woodsia* and *Diacalpe* have bristle-shaped pluricellular hairs, similar to those found on prothalli of Cyatheaceae. He regards the indusium of *Woodsia* as homologous with that of *Cyathea*, the globose *Diacalpe* indusium being still nearer to the *Cyathea* original. *Peranema*, with its zygomorphic sorus (the indusium slightly open on the side towards the edge of the lamina) is regarded as a type intermediate between the round sori of *Cyathea* and *Diacalpe* and the strongly zygomorphic sori of *Dryopteris*. These points are discussed in turn below.

Upright habit. This occurs in both Dicksoniaceae and Cyatheacaeae; in both cases it probably originated from the creeping habit. *Thyrsopteris* and *Lophosoria* both have erect stems, and both produce creeping runners, probably indicating a transitional stage from the creeping to the erect state. The genus *Ithycaulon*, very closely related to *Dennstaedtia* but with an upright stem, is most probably a later and independent development; and the erect habit has also been developed from the creeping habit in the *Pteris* tribe and in other groups of ferns. Thus the upright habit of *Dryopteris* is no indication of a Cyatheoid affinity.

Chaffy scales. The primitive Dicksonioid ferns are all hairy; but scales have developed independently in the *Lindsaya*, *Davallia* and *Pteris* tribes (probably also in the *Nephrolepis* tribe). Therefore the presence of scales in *Woodsia* is no bar to an origin from the hairy Dicksoniaceae, and the scales of *Dryopteris* (sens. strict.) are not closely similar to those of *Cyathea*, being like *Davallia* in their marginal teeth.

Pinnation of the leaves. Dicksoniaceae, *Dennstaedtia*, Cyatheaceae and the more primitive Dryopteroid ferns all have amply divided leaves. The oblique ultimate segments, with unequal base, of *Culcita*, *Dennstaedtia*, *Microlepia* and *Davallia* are far nearer to *Polystichum* and to many *Dryopteris* species than are Cyatheaceae, which have leaflets with almost equal base.

Open venation is characteristic of all these ferns, and gives no evidence on the present question.

Indusium. The indusium of *Dryopteris* and its allies is zygomorphic, symmetrical about the line of the vein upon which it stands, attached at the base of the sorus and open towards the margin of the lamina. The indusium of *Cyathea* is attached equally all round the base. Bower has a long section to explain the zygomorphy of the Dryopteroid sorus and its origin from the non-zygomorphic sorus of *Cyathea*. But if *Dryopteris* were derived from the *Dennstaedtia* stock, we should expect a zygomorphic sorus, as we have in *Davallia*, *Microlepia*, etc. We should then see the basal indusium of *Acrophorus* as primitive, and the globose indusium of *Diacalpe* as derivative. In *Oenotrichia* Copel. we have a genus vegetatively agreeing with *Dennstaedtia* and *Microlepia*, but with basally attached indusia which may be reniform. Here then we have a definite indication that the *Dryopteris* type of indusium can be produced by a *Dennstaedtia*-ally.

Gradate sequence of sporangia is found in *Dennstaedtia* and others of the more primitive Dicksonioid ferns; signs of a gradate sequence in primitive Dryopteroid ferns are therefore not inconsistent with a Dicksonioid origin.

Prothalli. Here we have later evidence, from A. G. Stokey (*Bot. Gaz.* vol. 90, pp. 1–45, 1930), who grew prothalli of Cyatheaceae, Dicksoniaceae and other ferns and compared them. She found that Dicksoniaceae lack the specialized bristle-hairs which are characteristic of Cyatheaceae; and that though hairs occur on the prothalli of *Woodsia*, *Diacalpe* and *Dryopteris*, they differ in origin and distribution from those of Cyatheaceae.

In Dr Stokey's opinion, this fact 'opposes rather than favours a genetic connexion' between the Dryopteroid genera and Cyatheaceae. The prothallus characters thus do not support Bower's theory.

Therefore Bower's evidence does not demonstrate the affinity of the Dryopteroid ferns with Cyatheaceae; on all points an affinity with *Dennstaedtia* is equally likely, or in some cases more likely, and the evidence of the prothalli is against him. There is further evidence, not mentioned by Bower, which points definitely to an origin from the *Dennstaedtia* stock.

DEPARIA Hook. & Grev. This genus, founded solely on indusial characters, unites three species which on all other characters belong to *Dennstaedtia*, *Athyrium* and *Tectaria*, and are usually placed in these genera by modern authors. For some inexplicable reason, having rejected the other artificial sorus-genera of the *Synopsis Filicum*, Bower retains this one. He places it among *genera incertae sedis*; but he indicates quite clearly that he considers it derived from *Dennstaedtia*.

The character upon which *Deparia* is based is the presence of marginal sori with a cup-shaped indusium of thin texture, which is not deflexed towards the lower surface of the frond as in most species of *Dennstaedtia*. It is certainly very near the *Dennstaedtia* sorus, and the species *Deparia Matthewsii* Hook. which agrees in other characters with *Dennstaedtia*, is reasonably included in the latter genus. But *Deparia prolifera* (Kaulf.) Hook. & Grev. has all the vegetative characters of *Athyrium*, and *D. Moorei* Hook. of *Tectaria*. Now if we assume that *Athyrium* (which is unquestionably closely allied to *Dryopteris*) and *Tectaria* have arisen from *Dennstaedtia*, there is nothing surprising in the fact that a few species should have retained the primitive sorus-form, though changing vegetatively. I submit that the existence of such species is evidence that the Dryopteroid ferns originated from ferns with marginal sori of the *Dennstaedtia* type. The alternative is to suppose that on entirely separate lines of evolution from *Dennstaedtia* the two species of *Deparia* have independently developed the vegetative characters of *Athyrium* and *Tectaria*; that is, independently of all the other species referred to those genera, assumed by Bower to have originated from Cyatheaceae.

RACHIS CHARACTERS. In *Culcita*, in some species of *Dennstaedtia* and *Hypolepis*, and in the Pteroid ferns (unquestionably of Dennstaedtioid stock) there is a uniform structure of costa and rachis and a uniform way in which they are related; and the only other known ferns which share this character are *Dryopteris* and its immediate allies, and *Athyrium* (with the exception that the less finely divided species of *Athyrium* do not show it clearly). The costa of a pinnule is grooved, with raised thin edges on either side of the groove. These raised edges are often interrupted at the insertion of the costules on the costae, and sometimes produced into teeth at these points (both in *Pteris* and *Athyrium*). Where the costa of the pinnule joins the pinna-rachis, the basiscopic edge of the groove of the costa joins the raised edge of the upper surface of the rachis, which is interrupted to receive it, and usually raised at the junction; the basiscopic edge of the lamina of the pinnule is decurrent on the side of the rachis, sometimes on to a lateral wing.

This uniformity, and a lack of a similar structure in other ferns, appears to me strong evidence of a relationship between *Dryopteris* (and *Athyrium*) and *Dennstaedtia*. There is also a strong resemblance in shape of leaflets between some species in the two genera, a much nearer resemblance than between the leaflets of *Cyathea* and *Dryopteris*; *Cyathea* also completely lacks the *Dryopteris* costa-rachis structure.

Taking then the zygomorphy of the sorus in *Dryopteris*, the existence of *Oenotrichia*, the persistent marginal sori of the species formerly grouped in *Deparia*, and the costa-rachis structure, together with the negation of a *Cyathea-Dryopteris* relation given by the prothalli, there appears to be strong evidence for an origin of *Dryopteris* and *Athyrium* from a *Culcita-Dennstaedtia* stock. The origin of *Athyrium* and *Tectaria* and their relation to *Dryopteris* is dealt with later. In the present tribe are included only *Dryopteris* and those other genera with similar anatomy and rachis-structure. A few of these call for comment.

POLYSTICHOPSIS. The species ranked here by Christensen differ from *Dryopteris* and from *Polystichum* in their anadromous leaf architecture, agreeing with *Dryopteris* in sori, while some have the aristate tough leaflets of *Polystichum* and some have leaflets more like *Dryopteris*. They are a difficult group to place; a solution might be found by uniting *Dryopteris*, *Polystichum* and *Polystichopsis* in one genus. Ching proposed to unite *Polystichopsis* with *Rumohra*, under the latter name; but *Rumohra* (as based on the only previously named species) has a creeping dorsiventral rhizome like that of *Davallia*, and fronds like those of *Davallia* in all respects except the peltate indusia. It is not nearly related to *Polystichopsis*. I suggest that it is near *Davallia*, and is another indication of the plastic nature of the indusium in Dennstaedtioid ferns.

DIDYMOCHLAENA. This is also an aberrant genus. It is pantropic, and little varied vegetatively, a fern of shady forest, and must be old. Its articulated pinnae and pinnules prevent the full development of the rachis-pinnule relations above described; but the main veins of the leaflets are not grooved, and the basiscopic edge of the leaflets is much thickened, just as in *Lindsaya*. There is also a curious group of spines at the base of each leaflet. The indusia are like stretched-out *Polystichum* indusia. It is probably a relative of *Polystichum*, but divergent at an early stage. A study of the development of the leaflets and their sori would be interesting.

10. TECTARIOIDEAE

GENERAL CHARACTERS

Rhizome erect or suberect, scaly, with complex dictyostele; *stipes* not jointed to it, containing several vascular strands.

Fronds amply divided to simple, either narrow in outline, or deltoid with basiscopically enlarged basal pinnae; costules and costae raised, not grooved; multicellular hairs usually present on upper surface of rachis, costae and other parts of frond; *veins* free or variously anastomosing.

Sori round with reniform or peltate indusia, terminal or dorsal on the veins; or without indusia, in which case they may spread along the veins; or acrostichoid.

GENERA. (*a*) *Ctenitis*, *Lastreopsis*, *Tectaria*, *Heterogonium*, *Quercifilix*, *Stenosemia*, *Cyclopeltis*, *Hemigramma*, *Amphiblestra*, *Pleuroderris*, *Dictyoxiphium*. (*b*) *Pteridrys*, *Pleocnemia*, *Arcypteris* (*Dictyopteris* Presl non Lamx.).

The basic genus of this tribe is *Ctenitis*, which in variation of frond form and in sori (as pointed out by Christensen) matches *Dryopteris* closely, but which differs constantly from *Dryopteris* in raised costae bearing many short multicellular hairs. I suggest that the two had a common origin (along with *Athyrium*) in the primitive *Dennstaedtia* stock, the ancestral form having grooved hairy costae (as in some species of *Dennstaedtia*), the *Dryopteris* tribe retaining the grooved costae but (except in some primitive genera) losing the hairs, the *Ctenitis* tribe losing the groove but retaining the hairs.

Tectaria is linked with *Ctenitis* by some species with free veins which were included in a separate genus *Ctenitopsis* by Ching; but they are so near *Tectaria devexa* that a separation seems unjustified. These primitive species of *Tectaria* have broader, fewer pinnae than *Ctenitis*, and the basal basiscopic vein of each group springs direct from the costa, not from the costule which bears the other veins. The majority of species of *Tectaria* have anastomosing veins, the extent and complexity of anastomosis progressing according to the broadening and simplification of the parts of the lamina, culminating in simply pinnate and simple-fronded species such as *T. polymorpha* and *T. singaporensis*. In these species the venation pattern closely matches that of the broad-leaved members of Polypodiaceae (sens. strict.), a remarkable case of convergent evolution. Some exindusiate species of *Tectaria* have even been referred to *Polypodium*; but the erect rhizome, non-articulate stipes and spores distinguish them.

LASTREOPSIS Ching is probably an offshoot from the deltoid-leaved species of *Ctenitis*; or it might be a genus of separate origin in the *Dennstaedtia* stock. It has a long-creeping rhizome which seems radial, not dorsiventral in structure, broadly deltoid fronds, the edges of the leaflets more or less thickened and decurrent on a wing to the rachis; the hairs on the upper surface of rachis and costae are like those of *Ctenitis* but stiffer. Ching wrongly placed this genus near *Thelypteris*. It appears to be distributed in south-east Asia, Malaysia and Australasia; all the species have not yet been recognized.

HETEROGONIUM is probably a distinct offshoot from *Ctenitis*, having more pinnae and narrower fronds than the primitive *Tectaria*. The existing species (9 or 10, Malaysian) have deeply pinnatifid pinnae, the lowest pinnae widest at about the middle (narrowed to the base). The veins are free or anastomosing in a series of costal areoles, in the largest species in further series of areoles also, with few if any included veinlets. The upper surface of the lamina bears scattered rather large multicellular hairs. Fertile fronds have a narrower lamina than sterile, and one species is acrostichoid; sori otherwise are as in *Tectaria*.

QUERCIFILIX and STENOSEMIA are acrostichoid genera of one species each, both derived from *Tectaria*, but evidently from different species of *Tectaria*, so that they must either be kept as separate genera or merged in *Tectaria* (the same problem arises as to the offshoots of the Polypodiaceae with peculiar fusion-sori).

DICTYOXIPHIUM is a monotypic tropical American genus which has long been associated with *Lindsaya* on account of its almost continuous marginal sorus, with indusium as in *Lindsaya*. Copeland (1941) states that it is an ally of *Tectaria*, and this alliance is proved by erect habit, scales, venation and spores (with winged perispore), in all of which it agrees with *Tectaria*, not with *Lindsaya*. Maxon (1934) remarks that his *Pleuroderris* is intermediate between *Tectaria* and *Dictyoxiphium*. *Amphiblestra* is also closely allied, having the habit of *Tectaria* and submarginal, often interrupted, exindusiate sori. *Hemigramma*, in the Philippines, is another peculiar local derivative of *Tectaria*, with very narrow fertile lobes or pinnae, and exindusiate sori in few close rows parallel to the margin.

CYCLOPELTIS is a genus of few species but wide distribution, occuring in tropical America as well as Burma and Malaysia. Its position as a member of the present tribe is doubtful, but it seems more likely to belong here than elsewhere. Lax *Ctenitis*-hairs are lacking, and the upper surface of rachises and costae is glabrous; there are very short hairs on the lower surface of the rachis. A relationship to *Polystichum*, on account of peltate indusia, has been considered probable by Copeland; but *Cyclopeltis* has little else in common with *Polystichum*. Its rhizome-scales are peculiar; and no other member of the present tribe has articulate pinnae. Further investigation of *Cyclopeltis* is desirable.

PTERIDRYS, PLEOCNEMIA and ARCYPTERIS form a distinct sub-group, characterized by the presence of prominent teeth (pointing out of the plane of the frond) in the sinuses between the pinna-lobes. These teeth give the living plants a very distinctive appearance, hardly seen in dried herbarium specimens, for which reason the three genera have not hitherto been associated. Hairs on rachises are less abundant than in *Ctenitis* and *Tectaria*, and are lacking in some species of *Pteridrys*, present in others at the junction of costae and rachis. Simple glandular hairs, yellow or red, are usually present on the lower surface of costules and veins in *Pleocnemia* and *Arcypteris*, and similar glands on paraphyses. The veins are free in *Pteridrys*; in *Pleocnemia* they unite in costal areoles, and in *Arcypteris* are more amply reticulate, without free included veins. A vein always passes to each sinus-tooth. These teeth are probably relics of an ancestral character in the *Dennstaedtia* stock. Somewhat similar teeth occur in *Egenolfia*, and they are indicated also in *Dryopteris sparsa* and other species. The sori are round, with reniform indusia or exindusiate.

PTERIDRYS. This genus was named on account of the resemblance of its venation to that of *Pteris* (group of *P. quadriaurita*); but its rachis-structure is quite different from that of *Pteris*, and no *Pteris* has the characteristic sinus-teeth of *Pteridrys* and its allies. In *Pteridrys* these teeth are sharper and more prominent than in the other two genera. The veins are free, a primitive character; and one of the Chinese species is quite a large fern, of size similar to *Arcypteris*, with long basal pinnules on the basal pinnae.

PLEOCNEMIA was founded by Presl on its venation only, for which reason Beddome and others added to the original species several of *Tectaria* which are not nearly allied but have veins uniting in a single series of costal areoles. The true *Pleocnemia* species have not received sufficient attention. Most have been referred to *P. Leuzeana* (called *Tectaria Leuzeana*); but in the Singapore herbarium alone some sixteen distinct species, ranging from Sumatra to Polynesia, are represented, three of them being native in the Malay Peninsula. There is no doubt that *Pleocnemia* is a very distinct genus; distinct in its very narrow rhizome-scales, its glandular hairs and sinus-teeth.

ARCYPTERIS is nearly allied to *Pleocnemia*, but less deeply dissected and with more elaborately reticulate veins. It has similar scales, glands and sinus-teeth, and the two might perhaps be united. There appear to be only three species. Like *Pleocnemia*, *Arcypteris* (as *Dictyopteris*) was defined on its venation and has had quite alien species referred to it. The original species had no indusia, and so Beddome used *Dictyopteris* as a dumping ground for all non-indusiate *Tectaria* (*Aspidium*) species.

11. ATHYRIOIDEAE

GENERAL CHARACTERS

Rhizome terrestrial, erect or suberect, of radial symmetry, scaly; stipes with two vascular strands at the base, uniting upwards to a single U- or V-shaped strand.

Fronds highly dissected to simple; *veins* nearly always free, or in a few species the veinlets of adjacent groups uniting to form parallelogram-shaped areoles; rachises and costae more or less scaly, hairless or the upper surface sometimes with thick multicellular hairs; *costules* and *costae* grooved, the edge of the groove decurrent upon the edge of a similar rachis-groove, the lamina decurrent on the side of the rachis.

Sori usually linear on the veins, with linear indusia, in some species reniform or J-shaped, in *Cystopteris* round with a basal indusium.

Spores with perispore.

GENERA: *Athyrium* (including *Diplazium*), *Cystopteris*.

Copeland has repeatedly urged the necessity of uniting *Diplazium* with *Athyrium*. After examining many species referred to both genera, I find myself in agreement with him that there is no obvious line of separation between them.

The supposed origin and development of the *Athyrium* indusium is discussed at length in comparison with that of *Asplenium* on an earlier page (p. 141). The matter is therefore not further mentioned here. *Cystopteris* is in all characters closely related to *Athyrium* except in the shape of the indusium.

It is suggested that *Athyrium* had a common origin with *Dryopteris* and its allies in *Dennstaedtia*, but that the two groups diverged at an early stage, *Athyrium* maintaining a simpler type of vascular anatomy than *Dryopteris*. The largest species of *Athyrium* (usually called *Diplazium*) are very large ferns, almost tree-ferns (none has more than a short erect stock) with fronds as large as any *Cyathea*. They are an extremely polymorphic group, evidently highly successful, mainly found as terrestrial ferns in primitive shady tropical forest. *Cystopteris*, on the other hand, is mainly a temperate genus, *C. fragilis* extending to the arctic (Christensen calls it the most widely distributed of all ferns).

Family ADIANTACEAE

GENERA as in Gymnogrammoideae C.Chr. with addition of *Taenitis*, and *Vittarioideae* C.Chr.

GYMNOGRAMMOIDEAE

Christensen follows in the main the same grouping as Bower (*The Ferns*, vol. 3, ch. 39). Copeland has a different arrangement, some points in which will be mentioned below. The group as a whole is large and varied, but the general tendency is towards xerophytism, with consequent reduction of size. Such ferns have little place in the Malayan climate; moreover, many of the genera are preponderantly American. I have therefore little first-hand knowledge of them, and can offer no fresh opinions on their inter-relations. The following is a brief summary of the views of other authors, with a more extended discussion only on the Malaysian genera *Syngramma* and *Coniogramme*, along with *Taenitis* which (in agreement with Copeland) I associate with *Syngramma*.

The sori of the Gymnogrammoid ferns are either terminal on the veins, or they spread for a longer or shorter distance along the veins; they have no indusium, but the edge of the lamina is sometimes reflexed to cover the young sori. Bower's contention is that there is no evidence that these ferns were derived from indusiate ancestors; Copeland considers that they were so derived. Bower derives them from Osmundaceae, Schizaeaceae or some allied primitive group; Copeland derives some from the alliance of *Lindsaya*, some from that of *Pteris*. Christensen is of opinion that there are several evolutionary lines within the group, most of them related to Pteroideae.

Bower's *first group* of genera consists of *Llavea*, *Cryptogramme*, *Onychium*, *Ceratopteris* and *Jamesonia*. These have on the whole primitive vegetative characters, but agree more definitely in having large, short-stalked sporangia with much inconstancy of the annulus, which is composed of many cells. The only one of these genera occurring in Malaya is *Ceratopteris*; this is specialized vegetatively to aquatic life, and has a complex vascular structure, though agreeing with the other genera in sporangial characters. Bower considers that this group of genera may have originated from some fern similar to *Todea*, and this seems a more probable suggestion than any other.

Bower's *second group* of genera is Christensen's Gymnogrammeae, without *Jamesonia*. In these genera, there is a general tendency for the sori to spread along the veins, in some of them throughout the whole length of the veins, giving in a few cases an acrostichoid appearance. The sporangia are of normal leptosporangiate type. The Malayan genera in this group are *Syngramma* (including *Craspedodictyum*), *Taenitis* (not included by Bower or Christensen), *Coniogramme*, *Pityrogramma*, and *Hemionitis*. Without knowing the last two genera at all intimately, my inclination would be to transfer *Pityrogramma* and probably also *Hemionitis* to the *Cheilanthes* group. The other genera seem to me nearly related, and are discussed in detail below. Bower devotes little attention to this group as a whole, merely describing *Trismeria* as an example, though it is not at all representative of the varied assemblage of genera. Copeland derives most of these ferns, but curiously not *Coniogramme*, from *Lindsaya* or its allies. Bower has little to say about their origin.

ADIANTUM is given a special place by Bower and Christensen. This is a large and isolated, very specialized genus. Copeland places it at the end of the *Cheilanthes* group (see below), which he derives from *Pteris*. Bower points out the peculiar thickenings in the cell-walls of the prothalli of *Adiantum*, *Cheilanthes* and *Pellea*, otherwise only known in the genera of Schizaeaceae; and the spicular epidermal cells of the sporophyte, a resemblance to the Vittarieae. I would agree that *Adiantum* is allied to the *Cheilanthes* group, but it is much less xerophytic than most of them, and the separation was probably an early one.

CHEILANTHES GROUP. This is the last group of Bower and Christensen; in Malaya it is represented only by *Cheilanthes* and *Doryopteris*, to which I suggest that *Pityrogramma* and *Hemionitis* are allied. In this group, as circumscribed by Bower, the sori are at the vein-endings; in some cases they spread laterally, and in *Doryopteris* the sori are continuous, a vascular commissure connecting the ends of the veins. The margin of the frond is often reflexed to protect the sori, as in *Hypolepis* and *Pteris*.

The general aspect of these ferns is thus much as in *Pteris*, from which genus (or near it) Copeland believes them derived, along with *Coniogramme*. Bower, on the other hand, suggests a derivation from Schizaeaceae. Against the derivation from *Pteris* is the fact that in *Pteris* there is a very regular vascular commissure in the sorus, and we must suppose the fusion-sorus with its vascular supply broken up again to produce such genera as *Pellaea* and *Notholaena*. And even in such a genus as *Doryopteris*, Prantl noted the difference from *Pteris* that the first sporangia are always produced at the vein-endings and only later sporangia between the veins, whereas there is no such order in *Pteris*. As Bower points out, fusion-sori have been derived on several evolutionary lines, and that of *Doryopteris* may be quite distinct from that of *Pteris*.

Another character which does not accord with the *Pteris* alliance for these ferns is the shape of the rachis. As pointed out elsewhere, in *Dennstaedtia*, *Hypolepis*, *Pteridium*, *Histiopteris* and *Pteris*, the midribs of the leaflets are deeply grooved with raised edges, these edges being decurrent upon the edges of the groove of the upper surface of the rachis, which is interrupted to receive them. This character does not appear in the *Cheilanthes* group of genera, nor in *Coniogramme*, though Copeland considers the latter very closely similar to *Pteris*.

Several authors have pointed out the resemblance of *Cheilanthes* and its allies to *Mohria*, a genus of Schizaeaceae. *Mohria* is advanced, as compared with other Schizaeaceae, in having scales instead of hairs, and in its vascular structure. It has single sporangia at its vein-endings, with the margin of the lamina reflexed to protect them as in *Cheilanthes*. A remarkable primitive ally of *Cheilanthes*, the genus *Sinopteris*, also has single terminal sporangia; this may well be an indication of Schizaeoid affinity.

SYNGRAMMA, TAENITIS AND CONIOGRAMME. Copeland has on several occasions pointed out the very close resemblance between *Syngramma* and *Taenitis*, which no one who has examined all the ferns in question could reasonably doubt; but Goebel completely ignores the relationship, and Bower goes so far as to associate the Malaysian *Syngramma* with the monotypic South American genus *Metaxaya*. But while I agree with Copeland so far, I completely disagree with him in his statement that *Syngramma* and *Taenitis* are probably derived from *Schizoloma*.

Copeland suggests that *Taenitis* is derived from an indusiate ancestor, and thus regards it as more primitive than *Syngramma*; but the reverse interpretation seems to me much more probable, namely that *Syngramma*, derived from non-indusiate ancestors by spreading of the sori along the veins, is the more primitive type, *Taenitis* being derived from it by condensation of the sori and their limitation to a narrow longitudinal zone. This seems to me a much more reasonable explanation than the derivation of *Taenitis* from *Schizoloma*, which would involve the loss of an indusium, the spreading of the sporangia along the veins back from the margin and their coalescence on a new line; or alternatively the disappearance of both indusium and vascular commissure and the extension of the lamina beyond the line of the sorus. Goebel rightly points out that the complete lack of the commissure gives the sorus quite a different structure from that of *Schizoloma*. Furthermore, *Schizoloma* lacks paraphyses, and these are found both in *Taenitis* and *Syngramma*. I see in fact no reasonable likelihood of the relationship suggested by Copeland; and consider that to find a common ancestor for all the genera one would have to go very far back, probably, as Bower suggests, to extinct primitive members of Schizaeaceae.

Copeland considers the bristles on the rhizome of *Taenitis* and *Syngramma* are an indication of immediate relationship with the *Lindsaya* group. But *Lindsaya*, *Schizoloma* and *Stenoloma* have distinctly flattened bristles or true scales, whereas the bristles of *Syngramma* and *Taenitis* are not flattened and are much more like those of *Dennstaedtia*. This bristle-character is in fact a primitive one in the stock from which *Dennstaedtia*, *Lindsaya* and the Pteroid ferns were derived, and its possession by *Syngramma* can at most mean a resemblance to the primitive members of the stock.

Copeland also expressly excludes *Coniogramme* from near relationship with *Syngramma*, mainly because *Coniogramme* has flattened scales (quite narrow ones) and *Syngramma* has bristles. But it is clear that on more than one line of descent from the primitive members of the *Dennstaedtia* stock there has been a development of scales from hairs, and it would not be surprising if it should occur on yet another line of evolution from primitive Schizaeoid ferns. Apart from the question of scales, there are other resemblances between *Syngramma* and *Coniogramme*; more, I should judge, than between either of them and any other genus except *Taenitis*.

The species of *Coniogramme* are large ferns, in some cases amply bipinnate; they are also ferns of primitive shady forest, usually in wet ground near streams, and they preserve a much more primitive frond form than those of *Syngramma*, which are nearly all much reduced and show some xerophytic characters, with adaptation to special habitats. I suggest in fact that *Coniogramme* gives us much better evidence as to the form of the ancestors of the group than does *Syngramma*; but that though *Syngramma* has become specialized by reduction of its fronds it has not developed flattened scales, whereas *Coniogramme* has done so. It is not rare to find that ferns more specialized than their relatives in some characters still preserve primitive features in other characters.

A difficulty certainly arises in the fact that *Coniogramme* has a much wider distribution than *Syngramma*. Further, *Syngramma* does not now occur in the region of the eastern Himalayas in which *Coniogramme* has the greatest number of species. *Coniogramme* can hardly be an older genus than *Syngramma*, but it has spread more widely, though it has produced comparatively little variety in vegetative form. *Syngramma* has perhaps been slower in extending its range owing to specialization of its species to limited habitats. The primitive leaf-form in *Syngramma* was presumably pinnate, as in the eastern Malaysian *S. pinnata*; but *S. pinnata* is more advanced than other species of the genus in having a copiously reticulate venation (it is in fact very near *Taenitis*). It is remarkable that the species of *Syngramma* with the widest distribution is *S. quinata*, which has the lateral leaflets basiscopically branched, a feature not seen in *Coniogramme*, though common in some of the Gymnogrammoid genera. In *Taenitis* such a branching occurs as an abnormality in an undescribed species from Malaya, but not otherwise. The smaller species of *Syngramma* (section *Toxopteris*), all with restricted ranges in western Malaysia, are evidently the most specialized species; none of them is common, and all are restricted to special habitats. It may be that, though restricted in range, they are not of very recent origin.

As noted above (in discussing the *Cheilanthes* group), the peculiar raised and grooved costae, with their edges decurrent on grooved rachises, of *Pteris* and the more primitive genera related to it, are not matched in the present group of genera; not even in *Coniogramme*, which has the most primitive frond form and might be expected to retain such characters. This appears to me strong evidence that *Coniogramme* and *Pteris* are not closely related. I suggest that *Coniogramme* resembles *Todea* and *Osmunda* more nearly than *Pteris* as regards frond form; and as regards structure of the leaflets and their relation to the rachis it is not far from *Lygodium*. I would in fact agree with Bower that *Coniogramme* probably originated from a stock allied to the Schizaeaceae, and that the *Dennstaedtia-Pteris* series had also a similar origin, but on a separate line of descent from an early stage. An origin from Osmundaceae, with their massive upright stocks, seems less likely.

VITTARIOIDEAE

This undoubtedly natural and apparently isolated group has been discussed at some length by Williams, whose work is summarized by Bower (ch. 47). I agree with Bower in the suggestion that *Hecistopteris* represents, in a very dwarfed state, the primitive form of the group, *Antrophyum* retaining a more primitive condition as regards size but with completely webbed lamina and reticulate veins. Bower remarks: 'The peculiarities which specially characterize these ferns are probably consequences of habit; in fact, the Vittarieae may be held to represent an epiphytic and rupicolous branch of specialization from a Gymnogrammoid source.' He goes on to refer to the spicule cells in the lamina, a feature otherwise only known in *Adiantum*.

The genus *Monogramme* represents a remarkable stage of reduction, its almost filiform fronds having one or few lateral veins, which are free. It doubtless arose from ancestors with reticulate veins (such as *Antrophyum*), and represents a parallel case to the small Polypodioid ferns which are free-veined descendants from reticulate-veined ancestors; free-veined because reduced in size of lamina.

AMENDMENT TO THIRD PARAGRAPH ON P. 134

Monachosorum is an anomalous genus, included here tentatively on account of its hairy rhizome. As pointed out by Hayata (*Flora*, vol. 124, p. 48, Fig. 9, 1930), the rhizome is erect, with dictyostelic radial structure, and two vascular strands to each leaf. The form of the frond corresponds in general with other members of the Dennstaedtioideae, with leaflets unequal at the base. The rachis is grooved, the edge of the groove raised and thickened where it opens to admit a leaflet; the costae of leaflets are not raised, in which character *Monachosorum* agrees with *Lindsaya* and *Leucostegia*. On the lower surface are shining large unicellular glandular hairs; on the bases of the stipes are hairs which are collapsed when dry, perhaps turgid when living. The sori are naked. Copeland placed this genus without comment in his Cyatheoid series; Christensen and Hayata thought it related to *Thelypteris*. In view of frond form, hairs, and rachis structure, and lack of scales, I do not think a relationship to *Thelypteris* likely. It is perhaps more nearly related to *Leucostegia* than to *Dennstaedtia*. Unfortunately fresh material of this genus is difficult to obtain.

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Polyploidy in Valeriana officinalis Linn. in relation to its ecology and distribution. By M. SKALIŃSKA

(With Plates 5–8, and 3 Text-figures)

[Read 10 January 1946]

INTRODUCTION

The present study was undertaken in 1942 at the suggestion of Dr T. A. Sprague as a renewed attempt to analyse the great morphological diversity within the collective species *Valeriana officinalis* L. In his paper (1943) Dr Sprague drew attention to the extremely wide range of forms occurring in the Cotswold Hills in a variety of habitats. On the whole, the plants investigated by him seemed to represent a more or less continuous series, rather than a small number of distinct types, such as those described by Drabble (1932) as separate species. According to Sprague's opinion this great diversity results from genetic differences, some of which might be due to polyploidy. The results of morphological studies by Dr B. Todd (1942), chiefly based on plants from the north of Great Britain, likewise yielded no evidence of the existence of a few sharply delimited species; she found, however, invariably the same chromosome number (56) in all plants which she investigated and which represented a wide range of forms. Plants with 28 chromosomes have since been detected in Britain (Skalińska, 1945).

The results of the present study have shown that the considerable range of forms in Britain within the collective species *V. officinalis* is due to three main causes: (1) phenotypic differences induced by external conditions; (2) differences in the number of chromosomes, 28 in tetraploids, 56 in octoploids; (3) a high degree of genic differentiation which brings about within each polyploid group a considerable number of forms with more or less distinct morphological differences.

Since the tetraploids, which presumably represent the older type, proved to be much rarer than the octoploids, special studies on the distribution and ecology in Great Britain of the two types were undertaken. These were based on field work combined with herbarium studies, and showed that the tetraploid type has a much smaller area than the octoploid and seems to be limited to the southern counties and parts of the Midlands, whereas the area of the octoploids extends from the southern counties to the north of Scotland. Ecologically, the tetraploids are distinctly separated from the octoploids, representing a xerophilous type, the occurrence of which is limited to a relatively dry soil in hilly regions.

The present studies were carried out in the Jodrell Laboratory of the Royal Botanic Gardens, Kew. I am greatly indebted to Sir Edward Salisbury, Director of the Kew Gardens, and to Dr C. R. Metcalfe, Keeper of the Jodrell Laboratory, for the facilities which enabled me to do the cytological part of the work and to grow my material in the garden. I wish also to express my sincere gratitude for the research grant awarded me by the Polish Fund of National Culture. Thanks are also due to Dr Sprague and others who collected materials and to curators of herbaria for the loan of specimens.

MATERIAL AND METHODS

Studies on living plants. In the course of the present work 115 living plants, transplanted from natural habitats to Kew, have been studied. These comprised 59 octoploid plants from 49 localities in fourteen Vice-Counties and 56 tetraploids from 36 localities in nine Vice-Counties.

The work on living plants included: (1) field studies of the plants in their natural habitats; (2) studies in the development and the morphological characters of the plants transplanted from their natural habitats into approximately uniform garden conditions (the plants were grown in Kew Gardens during three seasons 1943–45); (3) pollen measurements; (4) chromosome counts from root-tip mitoses.

In the first period the studies were limited to the material from the Cotswold Hills, which Dr Sprague sent me or which was collected together with him in a number of excursions. Subsequently the area explored was widened in order to get more details concerning the distribution of the two polyploid types in Great Britain, as well as their ecology.

Herbarium studies. In addition to investigations on living plants, specimens of *V. officinalis* L. in British herbaria were studied. The presumable chromosomic type of the specimens was estimated from the pollen size as well as from the morphological features which are often misleading. Originally this method of pollen measurement was worked out on living plants, on which the predictions could eventually be tested by chromosome counts. Owing to the distinct difference in the size of the pollen grains, this proved to be a reliable method for distinguishing the two chromosomic types. The comprehensive herbarium material provided in this way valuable information concerning the distribution and to some extent the ecology of the two types. In the preparation of this work specimens were examined in the following herbaria: Herbarium of the British Museum (Natural History), London; Herbarium of the Botany School, Cambridge; Welsh National Herbarium, Cardiff; Herbarium of the Dorchester Museum (collection of J. C. Mansel-Pleydell); Druce's Herbarium, Oxford; Herbarium of the Royal Botanical Garden, Edinburgh; Herbarium of the Royal Botanic Gardens, Kew; Herbarium of the Manchester Museum; Fielding Herbarium, University of Oxford; private collection of Mrs C. I. Sandwith and Mr N. Y. Sandwith in Clifton; Dr T. A. Sprague's collection of Valerians from the Cotswold Hills in the Kew Herbarium.

Abbreviations. In citing the specimens in the text, the following abbreviations have been used: Liv.Pl., living plant; H.Sp., herbarium specimen.

CYTOLOGY

The basic number of chromosomes in *V. officinalis* sensu lato is 7. Diploid as well as tetraploid and octoploid types have been found on the European continent. Previous results are summarized below:

V. exaltata Mik., $2n=14$ (Senjaninova, 1927).

V. rossica P. Smirn., $2n=28$ (Senjaninova, 1927).

V. volgensis L. Kazakewitsch, $2n=28$ (Senjaninova, 1927).

V. excelsa Poir. (= *V. sambucifolia* Mikan), $2n=56$ (Senjaninova, 1927).

V. officinalis L., $2n=14$, 28 (Runquist, 1937); $2n=28$ (Meurman, 1925); (probably *V. salina*, Asplund's material), $2n=56$ (Meurman, 1925).

V. salina Pleijel, $2n=56$ (Runquist, 1937).

As has been mentioned, the only chromosome number reported previously for the British Valerians by Todd was 56. In spite of these results, differences in the number of chromosomes was anticipated after preliminary pollen studies on some plants selected from Dr Sprague's material. The cytological examination of the first few plants proved the correctness of this anticipation, since tetraploid plants with 28 somatic chromosomes were detected in addition to octoploids which represent the commonest type. The total number of plants investigated cytologically in the course of the present work amounted to 115; the octoploid type was represented by 59 specimens, while the tetraploid number of chromosomes was found in 56 plants. According to the results summarized below, the tetraploids have a much smaller area of distribution than the octoploids:

	Vice-Counties	No. of plants investigated	Tetraploids	Octoploids
3	S. Devon	3	—	3
5	S. Somerset	2	—	2
6	N. Somerset	14	2	12
8	S. Wiltshire	4	3	1
9	Dorset	1	—	1
13	W. Sussex	1	1	—
17	Surrey	3	3	—
22	Berkshire	2	—	2
23	Oxon	8	2	6
24	Buckinghamshire	3	3	—
26	W. Suffolk	1	—	1
29	Cambridge	3	3	—
31	Huntingdonshire	1	—	1
33	E. Gloucestershire	52	37	15
35	Monmouth	2	2	—
39	Staffordshire	3	—	3
41	Glamorgan	3	—	3
44	Carmarthen	3	—	3
53	S. Lincoln	1	—	1
57	Derby	4	—	4
92	S. Aberdeen	1	—	1
	Total no. of plants	115	56	59

No. of Vice-Counties: tetraploids, 9; octoploids, 16.

POLLEN EXAMINATION

The measurement of the diameter of the pollen grains has been widely applied in the course of the present work for the estimation of the presumable chromosomic type of the herbarium specimens. In the octoploids the size of the pollen grains is larger than in tetraploids. Data obtained from the measurement of 109 pollen samples are given below (Table 1) in order to illustrate the differences between the two types.

TABLE 1

	Diameter of pollen grains (in μ)									n	Mean
	33 39	39 45	45 51	51 57	57 63	63 69	69 75	75 81	81 87		
Putative tetraploids (50 H.Sps.)	39	650	1223	203	11	—	4*	1*	—	2131	$46{\cdot}65 \pm 0{\cdot}05$
Putative octoploids (59 H.Sps.)	—	12	349	1289	924	104	14	1	1	2694	$55{\cdot}80 \pm 0{\cdot}07$

* Giant pollen grains.

It is evident that although the ranges overlap, the difference between the average values (9·15 μ) is reliable for the distinction of the two types. The results obtained led to the detection of several new habitats of tetraploids, living plants being subsequently collected there, and the chromosome counts confirming the predictions based on the pollen test. This method works successfully in all plants which have a fertile and normally developed pollen, and the results are not substantially affected by occasionally occurring slight disturbances (e.g. the presence of giant grains occasionally observed in the pollen of some plants; cf. Table 1). A few plants, however, had a highly abnormal pollen which seemed to result from some considerable disturbances in the course of development. Normal pollen grains are usually provided with three pores, whereas giant (unreduced) grains may have four pores. The abnormal pollen showed unusual differences of size

	Vice-Counties	Number of herbarium specimens investigated (pollen test)			
		Total	Putative tetraploids	Putative octoploids	Undefined
2	E. Cornwall	1	—	1	—
3, 4	Devon	8	—	8	—
5	S. Somerset	2	2	—	—
6	N. Somerset	10	3	7	—
7	N. Wiltshire	2	2	—	—
8	S. Wiltshire	1	1	—	—
9	Dorset	12	4	8	—
11, 12	Hampshire	3	—	3	—
13	W. Sussex	12	11	1	—
16	W. Kent	2	1	1	—
17	Surrey	13	8	5	—
19	N. Essex	1	—	1	—
20	Hertfordshire	8	7	1	—
21	Middlesex	1	—	1	—
22	Berkshire	7	4	3	—
23	Oxon	2	1	1	—
24	Buckinghamshire	4	1	3	—
25	Suffolk	1	—	1	—
29	Cambridge	4	3	—	1
30	Bedford	1	1	—	—
32	Northampton	1	—	1	—
33	E. Gloucester	26	13	13	—
34	W. Gloucester	6	5	1	—
35	Monmouth	16	11	3	2
38	Warwick	3	2	1	—
39	Staffordshire	2	—	2	—
40	Shropshire	3	—	3	—
41	Glamorgan	4	—	4	—
42	Brecon	4	—	4	—
43	Radnor	1	—	1	—
44	Carmarthen	1	—	1	—
45	Pembroke	2	—	2	—
46	Cardigan	1	—	1	—
47	Montgomery	1	—	1	—
48	Merioneth	1	—	1	—
49	Carnarvon	1	—	1	—
54	N. Lincoln	1	1	—	—
55	Leicester	1	—	1	—
56	Nottingham	2	2	—	—
57	Derby	3	—	3	—
58	Cheshire	1	—	1	—
62, 65	Yorkshire	3	—	3	—
81	E. Berwick	1	—	1	—
83	Edinburgh	2	—	2	—
90	Forfar	2	—	2	—
91	Kincardine	1	—	1	—
92	S. Aberdeen	1	—	1	—
97	W. Inverness	3	—	3	—
111	Orkneys	2	—	2	—
	Total	191	83	105	3

No. of Vice-Counties: tetraploids, 20; octoploids, 44.

within a single plant, the pollen diameter ranging from that of the smallest grains of tetraploids to that of the largest grains of octoploids, or even exceeding that size. Only three plants of this category were found among the herbarium material; two were collected on carboniferous limestone in the Wye Valley and one originated from Cherry Hinton, Cambridge. The means of the two former plants roughly correspond to the average values of octoploids. In the latter, however, the mean is intermediate between the respective values of the tetraploids and octoploids (mean = 51·84), thus suggesting that the plant is a hexaploid with 42 chromosomes. The existence of such a type, however, seems doubtful in view of the fact that the two types are intersterile. Thus, in a few instances it was impossible to draw any definite conclusions concerning the chromosomic type on the basis of pollen measurements. A similar phenomenon was observed once also in the pollen of a living octoploid plant from Cheddar Gorge (Liv.Pl. 137). Earlier stages of pollen development of this plant were studied with the method of acetolacmoid smears in order to elucidate the origin of the extreme size differences; it was found that giant (unreduced) pollen grains were formed rather frequently, and in the same anthers abnormally small grains seemed to result from a somewhat defective development caused by an abnormal thickening of the membrane. The wide range of variability is therefore combined here with a relatively low average value (mean = 51·87), in spite of the octoploid number of chromosomes. It is possible, therefore, that also the above-mentioned herbarium specimens represent octoploids.

Results of pollen measurements of 191 selected herbarium specimens are given on p. 162, comprising 83 putative tetraploids from 20 Vice-Counties, 105 putative octoploids from 44 Vice-Counties and, in addition, three undefined plants mentioned above.

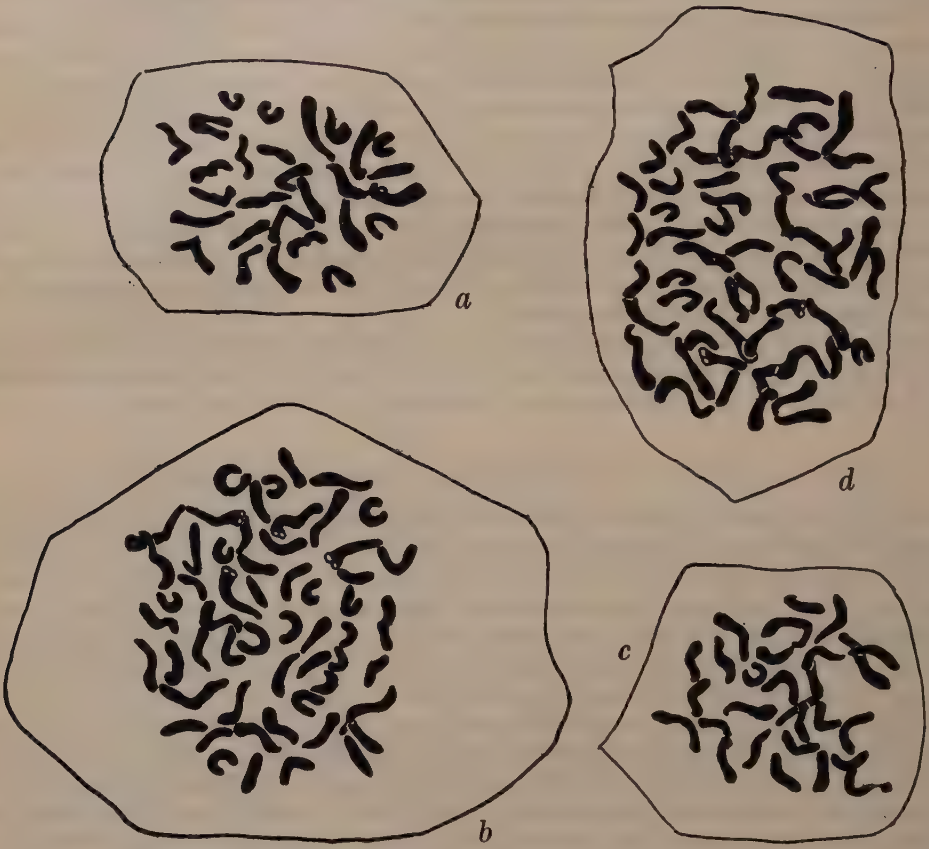
SOMATIC DOUBLING AND THE PROBLEM OF ORIGIN OF HIGHER POLYPLOIDS

In spite of the rather frequent occurrence of giant pollen grains observed in living plants as well as in herbarium specimens, no evolutionary value can be attributed to this phenomenon, since after pollination the unreduced pollen grains would be unable to compete with the normal pollen of the corresponding chromosomic type. On the other hand, it is probable that the production of a higher polyploid may be achieved by a spontaneous doubling of genomes in the somatic tissues. Such a phenomenon was observed in 1944 on one of the tetraploid plants from the Cotswold Hills, sent me by Dr Sprague in 1943 and planted at Kew. The somatic doubling was detected in a sector of the growing point of a sobole. This sector comprised about one-eighth of the periphery of a transversal section and had a length of about 100 μ, its cells and nuclei being larger than those of the normal cells of the meristematic tissues of a tetraploid. Two metaphases from this region, one with 28 chromosomes and another with 56 chromosomes, are represented (Text-fig. 1*c*, *d*). A further development of such a sector could give rise to a chimaera with a few octoploid shoots formed on a tetraploid plant. The doubling of chromosomes due to such a somatic polyploid mutation leads to the formation of a new type. In *Valeriana* among the factors which enable this newly formed type to persist, an important part is played by vegetative propagation. In sexual reproduction the barrier of incompatibility prevents intercrossing of the two polyploids.

MORPHOLOGY

The following characters have been studied in parallel series corresponding to natural habitats of the plants and culture in approximately uniform garden conditions: (1) morphology of the leaf—(*a*) number of pairs of lateral leaflets in the pinnate leaf, (*b*) shape of the lateral leaflets (ratio width/length and some other details), (*c*) degree and type of toothing of their margins; (2) morphology of the flowering stem—(*a*) height and thickness, (*b*) pubescence, (*c*) presence of anthocyanin; (3) time of flowering.

In the course of these studies adult plants from natural habitats were described and usually preserved in the form of herbarium specimens for further comparative studies. Young plants arising from the underground runners of the same plants were planted for cytological studies and for morphological examination. A group of plants from the same colony in a given locality was given a common field number, or letter, corresponding to that of the respective herbarium specimen and, in addition, each plant had its individual number. Small colonies usually represented clones and were morphologically perfectly uniform; on the other hand, in larger groups some amount of diversity was always observable both in nature and culture. Plants originating from different habitats showed sometimes well-marked character differences which were retained under conditions of cultivation, this being an indication of their genetic basis.



Text-fig. 1. Somatic metaphases of tetraploids and octoploids: *a*, plant 4, a tetraploid with relatively broad, conspicuously toothed leaflets (Withington Road, Glos.); *b*, plant 8/3, a giant octoploid plant with very broad leaflets (Sapperton, Glos.); *c*, plant H, a tetraploid with narrowly lanceolate leaflets (Withington Road, Glos.); *d*, metaphase from an octoploid sector of the same plant. (Navashin-gentian violet.) (× 2800.)

Morphology of the leaf. The characters of the leaves have been studied on stem leaves of flowering plants, these being more suitable for studies than the basal leaves, owing to a higher degree of stability. On the other hand, the basal leaves represent a series ranging from juvenile forms to those more or less similar to the stem leaves. In spite of some variability observable between the stem leaves of a single plant, certain details of their morphology seem to be well defined and to find a parallel expression in plants grown in natural habitats and in garden culture. In the upper part of the flowering stem there is usually a transition to simpler forms, and in the region of the inflorescence the leaves are replaced by bracts. In studying the number of pairs of lateral leaflets such partially reduced leaves were not taken into consideration.

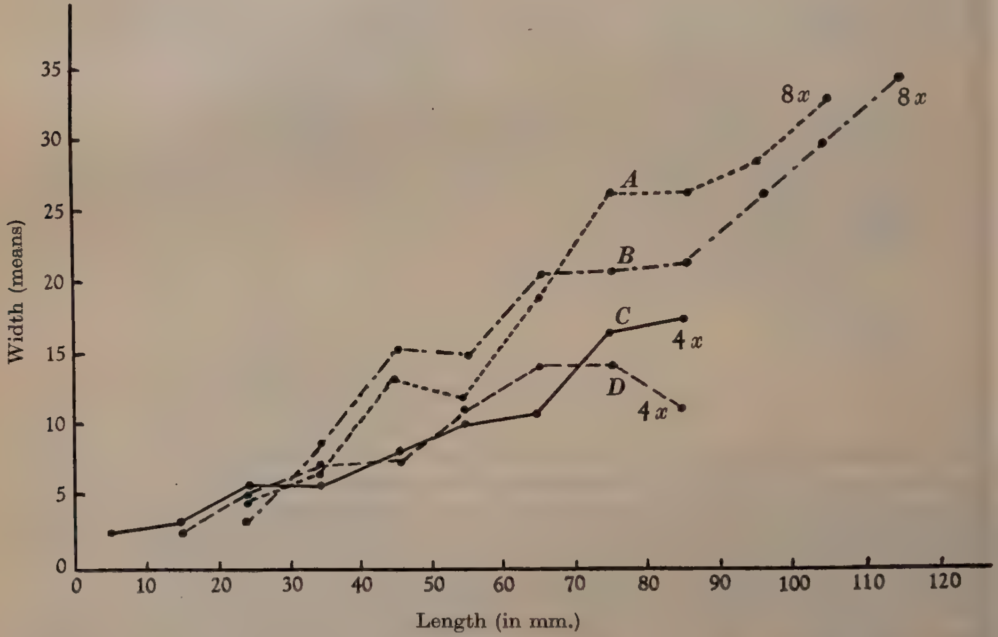
(*a*) *The number of pairs of lateral leaflets.* The occurrence of distinct types with lower numbers and of others with higher numbers of lateral leaflets has been established on the basis of the study of plants in nature, the extremes being connected by a range of intermediate forms. In the tetraploids, the number of pairs ranges from 5 to 10 (modal class = 7); in the octoploids the range extends from 3 to 10, the higher numbers 9 and 10 being, however, extremely rare (modal class = 5). On the average, the tetraploids have a somewhat higher number than the octoploids (cf. Table 2), but owing to the strong overlapping of these characters, it seems impossible to distinguish on this basis the two polyploid types except for the plants with 3 and 4 pairs which are always octoploid. The comparison of plants from natural habitats with the corresponding specimens in culture has shown that the number of pairs of lateral leaflets represents a relatively stable character; thus the diversity within each chromosomic type should be attributed to genic differences.

TABLE 2. *Number of pairs of lateral leaflets*

No. of pairs...	3	4	5	6	7	8	9	10	*n*
Living plants:									
Tetraploids	—	—	4	14	**16**	8	3	2	47
Octoploids	2	9	**16**	15	5	5	2	1	55
Herbarium specimens:									
Tetraploids*	—	—	5	6	**16**	12	7	6	52
Octoploids*	2	8	**26**	21	10	2	1	2	72

* Chromosomic type estimated from pollen tests.

(*b*) *The shape of the leaflets.* This character shows a great diversity, the extreme forms being connected by a range of intermediates. The various shapes presumably result from combinations of a number of independently transmitted polymeric genes for length and width. In octoploids the range is wider than it is in tetraploids, in accordance with the greater number of possible combinations of genes. The general shape of the leaflets is determined by the ratio width/length; in linear and narrowly lanceolate leaflets this ratio ranges from 0·12 to 0·20 (cp. Pl. **7**, fig. 6), in lanceolate and broadly lanceolate leaflets it increases gradually to 0·30 (Pl. **7**, fig. 4 and Pl. **8**, fig. 8), and in ovate leaflets it exceeds this value and may attain in extremely broad leaflets 0·40–0·50 (Pl. **8**, fig. 10). The photos of the leaflets (Pls. **7** and **8**) give some idea of the wide range of forms in the two polyploids. It is evident that in many instances a correct estimation of the chromosomic type on the base of the leaflets' shape is impossible. The comparison, however, of the two series, separated from one another by cytological methods, reveals the existence of differences between them. The tetraploid series begins with linear and narrowly lanceolate leaflets (Pl. **7**, fig. 6) which are followed by lanceolate and broadly lanceolate leaflets (Pl. **7**, figs. 4, 7). The ratio width/length of the former ranges from 0·12 to 0·20, and of the latter from 0·21 to 0·27, but in a few plants with still broader leaflets this value may reach 0·30. The octoploid series has, on the whole, a wider range of forms, the extreme types with linear or narrowly lanceolate leaflets being practically indistinguishable from the corresponding types in tetraploids (Pl. **7**, fig. 6); these forms, however, are rather infrequent. The next members of the series are represented by lanceolate and broadly lanceolate leaflets and some of these forms are also similar to those of tetraploids; more frequently, however, a rather distinct increase in width in proportion to length is observable. In such leaflets the ratio width/length is accordingly higher than in the broadest leaflets of tetraploids, reaching in extreme forms the value 0·50. These very broad leaflets at the end of the octoploid series usually attain a considerable size, the largest leaflets in the living material investigated belonging to giant plants of the *sambucifolia* type; e.g. the leaflets of plant M.8, reproduced in Pl. 8, fig. 10, is 115 mm. long and 40 mm. wide, and the ratio width/length is 0·347. In tetraploids, the largest leaflets were found in plant T.4 (Pl. 7, fig. 7), the length being 82 mm., the width only 19 mm., the ratio width/length 0·231, and consequently the difference in the shape is distinct. The type corresponding to *sambucifolia* is missing in the tetraploid series. This is evident from the graph (Text-fig. 2), which shows the range of forms and sizes of the leaflets of the two polyploid series. In the part corresponding to small and narrow leaflets the graphs closely coincide with one another, whereas in the parts corresponding to intermediate forms they show a steadily increasing divergence. The last part of the graphs in the octoploid series corresponds to leaflets which



Text-fig. 2. Four graphs representing the range of shapes and sizes of the leaflets of tetraploids and octoploids: A, octoploids from natural habitats; B, octoploids grown at Kew in approximately uniform garden conditions; C, tetraploids from natural habitats; D, tetraploids grown at Kew in approximately uniform garden conditions.

exceed the greatest length and width of the leaflets of tetraploids. This series ends with the extreme forms of giant *sambucifolia*, the latter form linking up with the octoploid *officinalis* type by a range of intergrading forms which, likewise, have no corresponding forms among tetraploids.

(*c*) *The toothing of the margins of the leaflets.* Both in octoploids and in tetraploids the margins may be either entire, or only the basiscopic margin may be slightly toothed, or the toothing may occur on both margins. The shape and size of the teeth, as well as their distribution along the margins, show a higher degree of differentiation in octoploids than in tetraploids. A coarse toothing has been observed in most of the extreme *sambucifolia* plants. Various types of toothing are represented on the photos (Pls. 7 and 8). In general, the type of toothing is relatively stable and is retained under conditions of cultivation. A genetic analysis of the toothing is impossible without breeding experiments; at least, several Mendelian factors seem to play a part in the determination of this character.

MORPHOLOGY OF THE FLOWERING STEM. (*a*) *Height.* The height of the flowering stem has a genetic basis and seems to be determined both by genic structure and by the number of genomes, but in nature its development is strongly influenced by the environment. In some extreme habitats the plants are dwarfed or sometimes they are unable to develop a flowering stem and such stunted forms, represented in nature only by tetraploids, could develop normal flowering stems after transplanting. In cultivation the range of forms was still considerable although not as wide as in nature. The high degree of diversity within each group and the relative stability of some strains suggest the existence of genic differences. In octoploids, the diversity is greater than in tetraploids, the range showing a degree of asymmetry due to the presence of some giant plants of the *sambucifolia* type, the smallest octoploids having slender, thin stems and being sometimes indistinguishable from tetraploids (Pl. 6, fig. 3). In tetraploids the most common type is represented by slender plants, 50–90 cm. high, but occasionally, however, tall and vigorous plants have been found in the material investigated (Pl. 5, fig. 1). Owing to the strong overlapping of the ranges, the height of the flowering stem cannot be regarded as a reliable character for the distinction of the two polyploid types, even if the plants are grown in approximately uniform garden conditions (Pl. 6, fig. 2). The difficulty of a correct estimation of the chromosomic type of specimens from nature is still greater in view of the strong influence of some extreme habitats. Octoploids occurring on limestone (e.g. specimens from Cheddar Gorge) have short and slender stems and in their general habit are very similar to tetraploids. On the other hand, some extremely vigorous tetraploids in the Cotswold Hills develop tall and stout stems which in extreme plants exceed 150 cm. in height and are 10–12 mm. thick. Such plants may be easily mistaken for octoploids.

TABLE 3

	Height of the flowering stem (cm.)														
	0*	10–30	30–50	50–70	70–90	90–110	110–130	130–150	150–170	170–190	190–210	*n*	$M \pm m$	σ	*v*
Natural habitat:															
Tetraploids	8	2	5	8	8	4	2	1	1	—	—	39	74·2 ±4·64	25·6	34·5
Octoploids	—	—	5	15	9	2	3	2	1	1	1	39	82·05 ± 3·20	20·8	25·2
Culture:															
Tetraploids	—	3	24	29	39	15	3	—	—	—	—	113	68·71 ± 1·67	17·8	20·6
Octoploids	—	—	8	19	25	17	14	7	5	1	—	96	91·66 ± 2·63	26·0	28·3

* Stunted plants without flowering stem.

It should be added that most of the plants studied in the course of the present work originated from the south of England and from the Midlands. In view of the fact that a number of living plants was received from the collectors in the stage of rosettes, the height of the respective specimens in their natural habitats was unknown. On the other hand, a number of flowering specimens, collected in 1945, did not yet flower in garden culture. Thus, the data in Table 3 do not represent corresponding series. The comparison of the same plants in nature and in garden culture is given later (Table 12).

(*b*) *Pubescence.* In the two polyploids the extremes, the glabrous and the strongly pubescent stem, are connected by a range of intermediate forms. Therefore, the range has been arbitrarily divided in the following four classes: (1) the stem glabrous or sometimes the first internode slightly pubescent; (2) the first two internodes moderately pubescent, the upper part of the stem almost glabrous; (3) the lower half of the stem distinctly pubescent, the upper only slightly pubescent; (4) the stem strongly pubescent from the bottom to the top. Plants in garden culture at Kew have been studied and classified according to this scheme. The respective figures are given in Table 4; they show that the extremes are present in tetraploids and in octoploids. In general, however, the pubescence is more strongly expressed in the tetraploids, and also the frequency of strongly pubescent plants is higher in this type. The differences in the degree of pubescence observable in approximately uniform conditions have presumably a genic basis. Some degree of diversity in this respect may sometimes occur within a strain (cp. Table 8); on the other hand, members of clones are always perfectly uniform with regard to the degree of pubescence of the stem. In octoploids there is a prevalence of plants with glabrous stems (class 1), whereas in classes corresponding to higher degrees of pubescence the frequency gradually decreases. Extreme *sambucifolia* plants belong to the two first classes. It is interesting to note that the only strongly pubescent octoploid plant (class 4) had its natural habitat by a permanent spring in swampy ground in an alder-ash copse (Hilcot Wood, Cotswolds, coll. Dr T. A. Sprague). This belonged to an isolated octoploid colony in the midst of a tetraploid area. In tetraploids a moderate and distinct pubescence of the stem (classes 2 and 3) represents the most common types, whereas the extremes are less frequent.

TABLE 4. *Pubescence of the stem*

	Degree of pubescence (cp. text)			
	(1)	(2)	(3)	(4)
Tetraploids:				
No. of plants	6	16	17	4
Percentage	13·94	37·20	39·52	9·35
Octoploids:				
No. of plants	26	11	8	1
Percentage	56·52	23·93	17·39	2·17

The above observations refer to living plants grown at Kew. A similar differentiation has been found among living specimens collected in nature in 1945, and thus not included in the groups grown at Kew. For example, of nine octoploid specimens from a variety of habitats in Cheddar Gorge, seven plants had glabrous stems, and in two the first internodes were slightly pubescent (coll. N. Y. Sandwith and M. Skalińska). In the Avon Valley below Bristol, where both octoploids and tetraploids were found, the former had glabrous stems and the latter (two groups of plants) had distinctly pubescent (class 3) or strongly pubescent stems (class 4). A detailed examination of herbarium specimens in this respect was not undertaken, but occasionally some differences in the degree of pubescence were observed among plants collected together in the same locality. For instance, two plants (putative tetraploids) from the borders of a copse, Amberley, West Sussex (coll. W. C. Barton, 1917, Br.Mus.), represented two distinct types with regard to pubescence, one having a glabrous stem and the stem of the other being distinctly pubescent (class 3). A living specimen from the same locality has been studied by me in 1945 (coll. N. Y. Sandwith and S. Batko); it was a tetraploid of the same morphological type with a still stronger pubescence (class 4). This suggests the existence of genic differences in respect to the degree of pubescence, within non-uniform populations.

(*c*) *Presence of anthocyanin.* Both the tetraploids and the octoploids show some amount of differentiation with regard to the coloration of the flowering stem. The two extremes, pure green and dark red stems, are connected by a range of intermediate forms. As is well known, the development of anthocyanin and the intensity of coloration is strongly influenced by external conditions such as temperature, moisture, intensity of light. It is evident that even in approximately uniform conditions of cultivation the above external factors unavoidably show some variability during the season and may affect in various ways the development of the pigment in the flowering stem of early, intermediate and late-flowering strains during their development. In view of this, the grouping of the material was difficult. It could be assumed, however, on the basis of observations during two seasons, that, despite the considerable variability, a paler or darker coloration of the stems results from genic differences. It is probable that they are due to polymeric factors controlling the intensity of the coloration of the stem; probably a larger number of genes is involved, and in each polyploid type a range of combinations may be formed. Breeding experiments are required for a genetic analysis of this character. A morphological analysis of the material grown at Kew gave the following results. The material has been grouped arbitrarily in four classes: (0) anthocyanin absent, stems green; (1) traces of anthocyanin in the stems; (2) anthocyanin present, stems brownish green; (3) stems intensely coloured (dark red). Table 5 gives the frequencies in the four classes for the two chromosomic types. The high degree of conformity in the frequencies of the corresponding classes of tetraploids and octoploids should not be overestimated. It is probable that a more precise study would allow us to distinguish more than three degrees of anthocyanin coloration, chiefly in octoploids, which presumably are able to form more genic combinations owing to their higher number of genomes. It is, however, evident from the results obtained that the different classes of coloration of the stem have approximately the same frequencies in the two polyploid types.

Table 5. *Presence of anthocyanin in stem*

	Classes of coloration of the stems (cp. text)			
	(0)	(1)	(2)	(3)
Tetraploids:				
No. of plants	11	14	7	8
Percentage	27·5	35·0	17·5	20·0
Octoploids:				
No. of plants	11	12	8	10
Percentage	26·83	29·26	19·52	24·39

In connexion with the presence of anthocyanin in the stem, a few words may be added in respect to the coloration of the buds and the flowers. In most cases plants with dark red stems bear purplish buds and bright pink flowers (the colour of the buds is usually more intense than that of the expanded flowers); on the other hand, plants without anthocyanin in stems have very pale buds and flowers. In some strains, however, plants with dark red stems have been found which, nevertheless, had pure white buds and flowers, whereas in some others which had only traces of anthocyanin in the stems the flowers were more or less intensely coloured. It is noteworthy that these two unusual combinations have been found in a mixed population of tetraploids in the same locality (Shewel in Cotswold Hills; coll. T. A. Sprague and M. Skalińska). It is probable that they represent some very rare combinations of genes.

The size of the inflorescences seems to vary in connexion with the general vigour of the plants rather than their chromosome numbers. In large plants, both tetraploids and octoploids, they may attain a considerable size. Concerning the shape of the inflorescences, two types may be distinguished: loose, richly branched inflorescences and others with relatively short ultimate branches and therefore with more densely grouped individual flowers.

Time of flowering. In nature the time of flowering is greatly influenced by the habitat, and therefore the observations from nature are not reliable for the study of the genetic basis of this character. For this purpose the various strains of octoploids and tetraploids grown in approximately uniform garden conditions were studied and records were taken at regular time intervals during two seasons (1944, 1945). These studies showed that each polyploid type represents a mixture of early-, intermediate- and late-flowering strains.

Early strains begin their flowering between 25 May and 10 June; the corresponding dates for intermediate strains are 10 and 25 June, whereas the late-flowering strains develop their first flowers between 25 June and 10 July. In spite of some variations, the records of 1945 confirmed the observations of the previous year. In general, the beginning of flowering seems to represent a relatively stable character, and within a clone the separate plants begin their flowering almost simultaneously, sometimes with a few days' interval. In strains with some amount of genic differentiation more or less distinct differences with regard to the beginning of flowering could be observed.

The tetraploids studied were composed of 13 early-, 16 intermediate- and 5 late-flowering strains. Sometimes quite different strains originating from the same area showed a perfect conformity with regard to the time of flowering. Two early strains from Wyndcliff and Chepstow, two intermediate strains from two remote localities in the Chilterns, and three intermediate strains from three localities in the Wiltshire Downs may be mentioned here: they are all tetraploid. On the other hand, sometimes different clones, or strains in the same locality, show some differences in this respect. In the Cotswold Hills, at Sapperton, six early tetraploid clones showed only slight differences in the beginning of their flowering and one tetraploid clone was somewhat later flowering, whereas three octoploid clones from the same locality represented late-flowering types. Another example of such a differentiation has been observed among plants from five habitats in and around Chatcombe Wood in the Cotswold Hills: in nature, only in two habitats were the plants able to flower, in the other three they were stunted; in culture, one of the stunted plants belonged to the earliest among early-flowering strains (first flowers between 25 and 30 May), one was intermediate and one was late-flowering. The first of the two plants which flowered in nature was early in culture, and the second—a very vigorous and tall plant—was intermediate. A distinct diversity with regard to the time of flowering could be observed among plants from Withington Road, a dry valley east of Lower Hilcot in the Cotswold Hills. Among the mixed population with the prevalence of intermediate plants some late-flowering individuals were also found.

The octoploids were represented in the material studied by 8 early-, 17 intermediate- and 9 late-flowering strains. The earliest strains were represented by tall and vigorous plants from swampy ground in Oxon and Somerset. The latest strain was native in Aberdeen, its plants belonging to the smallest octoploids in culture (Pl. **6**, fig. 3).

Data concerning the beginning of flowering in tetraploids and octoploids are summarized in Tables 6 and 7.

TABLE 6. *Flowering of tetraploids*

	Beginning of flowering											No. of strains or clones
	May		June						July			
	26	31	5	10	15	20	25	30	5	10	15 20	
(*a*) Early strains:												
Cotswold Hills	9	16	25	7	—	—	—	—	—	—	—	11
Wye Valley	1	4	—	—	—	—	—	—	—	—	—	2
(*b*) Intermediate strains:												
Cotswold Hills	—	—	—	13	13	—	1	2	—	—	—	7
Cambridge	—	—	—	3	—	1	—	—	—	—	—	2
Wiltshire Downs	—	—	—	—	2	1	—	—	—	—	—	3
Oxon	—	—	—	—	—	1	—	—	—	—	—	1
North Downs	—	—	—	—	—	3	—	—	—	—	—	3
(*c*) Late strains:												
Cotswold Hills	—	—	—	—	—	—	3	4	1	—	—	3
Chiltern Hills	—	—	—	—	—	—	—	3	—	—	—	2
Total no. of plants: 113	10	20	25	23	15	6	4	9	1	—	—	

A few words should be added concerning the morphology of the early- and late-flowering strains. In tetraploids neither the vigorous development of the stem, nor a special shape of the leaflets, is correlated with the time of flowering: plants with tall stems and relatively broad leaflets are found both among early- and late-flowering strains, and the same is true for the common type with slender stem and narrow leaflets. Plants which in natural habitats are unable to flower, in culture may represent very early-, or alternatively, very late-flowering types. In octoploids, all the early-flowering plants were vigorous, but likewise no definite form of leaflets was correlated with the time of flowering. Leaflets of early-flowering octoploids are represented on Pls. **7** and **8**.

TABLE 7. *Flowering of octoploids*

	Beginning of flowering											No. of strains or clones
	May		June						July			
	26	31	5	10	15	20	25	30	5	10	15 20	
(*a*) Early strains:												
Oxon	1	1	—	—	—	—	—	—	—	—	—	2
Somerset Levels	1	1	—	—	—	—	—	—	—	—	—	2
Dovedale	—	4	—	—	—	—	—	—	—	—	—	1
Wales (Carmarthen)	—	—	4	—	—	—	—	—	—	—	—	1
S. Devon	—	—	3	—	—	—	—	—	—	—	—	1
Berkshire	—	—	4	4	—	—	—	—	—	—	—	1
(*b*) Intermediate strains:												
Cotswold Hills	—	—	—	6	9	4	—	1	1	—	—	7
Oxon	—	—	—	3	—	1	—	—	—	—	—	2
Pennines (Derby)	—	—	—	2	—	—	—	—	—	—	—	1
Staffordshire	—	—	—	2	2	1	—	—	—	—	—	2
Wales (Glamorgan)	—	—	—	3	—	—	—	—	—	—	—	2
Wiltshire	—	—	—	—	4	—	—	—	—	—	—	1
Dorset	—	—	—	—	4	—	—	—	—	—	—	1
S. Devon	—	—	—	—	1	2	2	—	—	—	—	1
(*c*) Late strains:												
Cotswold Hills	—	—	—	—	—	—	9	6	—	—	—	4
Derby	—	—	—	—	—	—	1	1	—	—	—	2
Wales (Carmarthen)	—	—	—	—	—	—	—	2	2	—	—	2
Aberdeen	—	—	—	—	—	—	—	1	1	1	1	1
Total no. of plants: 96	2	6	11	20	20	8	12	11	4	1	1	

Among late-flowering plants, extreme morphological differences may be found: a distinct, although non-uniform group of giant plants with large leaflets (three strains from Sapperton, Cotswolds) (Pl. **8**, fig. 10), and, on the other hand, extremely small plants with very narrow leaflets (a strain from Aberdeen), (Pl. **6**, fig. 3) belong to late-flowering types.

In natural habitats the octoploids seem to display a greater variability in respect to the beginning of their flowering period than do the tetraploids. This is presumably due to the fact that the area of distribution of the octoploids is much larger than that of tetraploids, and consequently a greater variability may be attributed, at least to some extent, to latitudinal influences (in the north of Great Britain) or to the external conditions at higher altitudes. In the material studied there were some plants which in nature flowered much later than in culture. Flowering plants of a strain from the Pennines were collected on 16 August 1944; in garden culture this strain developed its first flowers already between 10 and 15 June. It is probable, however, that, in addition to the environmental influences, the genic structure is responsible for the very late flowering of some strains. The plants from Aberdeen, received at the end of August 1943, were in flower; in their native locality the flowering may be delayed under the influence of the environment, but als in conditions of cultivation at Kew during two seasons these plants flowered lat (cp. Table 7) though earlier than in nature and seemed to be ill-adjusted to the externa conditions at Kew. This suggests the existence among the octoploids of genic difference between strains occurring at different latitudes, but this problem requires further study

In general, the results obtained from the study of the features of the two polyploi types show clearly that in most cases purely morphological criteria are inadequate fo a correct delimitation of the two types. This is due to a great diversity within each grou and a strong overlapping of all the characters analysed. Only a few characters have limited diagnostic value (viz. the shape and size of the leaflets, the number of pairs in th pinnate leaf, and, in a still lower degree, the pubescence of the stem). These character may help to identify with certainty only the extremely vigorous forms of octoploids rep resented by the so-called *sambucifolia* type, this being due to the fact that in the series o tetraploids a corresponding type is missing.

E. Drabble (1932) distinguished three separate species within the collective specie *V. officinalis* Linn. in Great Britain, *V. angustifolia* Host, *V. officinalis* Linn. and *V* *sambucifolia* Mikan. Recent studies (Todd, 1942; Sprague, 1943) have shown that owing to the great diversity and the occurrence of intergrading forms, *V. officinalis* sens lato must be regarded as a single polymorphic species. As far as the interrelations of thes three species of Drabble are concerned, it has been pointed out by Sprague (p. 94) tha there are greater morphological differences between *V. sambucifolia* and *officinalis* tha between *officinalis* and *angustifolia*. The results of the present study strongly suppor this opinion. It seems plausible that the extreme giant *V. sambucifolia* is phylogeneticall a more or less separate group consisting exclusively of octoploid plants. On the othe hand, the plants ranging from *angustifolia* to *officinalis* s.str. seem to represent a series o closely related forms. This series consists of two chromosomic types, the tetraploids and th octoploids. In addition to polyploidy, purely genic differences contribute to increase th morphological diversity within the group. The occurrence of corresponding forms o tetraploids and octoploids suggests their common origin; they might have arisen as th result of chromosome doubling which could have taken place not once but severa times in different, though closely related, forms. Other octoploids, however, namely those plants which represent intermediate forms between *officinalis* and *sambucifolia* have presumably a different origin; they might have arisen by hybridization followed b segregation of some octoploid *officinalis* plants with the extreme giants of *sambucifolia* A number of forms of such a heterogeneous progeny could be fixed by vegetative propagation as permanently hybrid clones. A still greater degree of morphological diversity i the offspring could be attained by repeated cross-pollination. On the whole, the polymorphic species *V. officinalis* sensu lato seems to represent a mixture of autotetraploid with auto- and allooctoploids.

It is evident from the examination of a large number of specimens that none of th three species of Drabble is really uniform with regard to morphology. Cytologically only *V. sambucifolia* corresponds to a definite chromosomic type, whereas his two othe species show a polyploid differentiation. Of three specimens of *angustifolia* in Druce' Herbarium quoted by Drabble, two are putative octoploids (plants from How Wood Essex, coll. A. H. Wolley-Dod, and from Doveholes, Dovedale); the third plant (fro Wyndcliff) is probably a tetraploid. Among living plants of the same type investigate in the present study, both tetraploids and octoploids have been found (cp. Pl. 7 fig. 6): for example, tetraploids from the Wyndcliff, Mon. (Pl. 112), Shewel, Glos (Pl. T. 11) and Caterham, Surrey (Pl. 117); octoploids from Cheddar Gorge (Pl. 136 and Aberdeen (Pl. 19). It may be added that both among herbarium specimen and the living plants investigated cytologically, there was a range of forms linkin up with forms assigned by Drabble to *V. officinalis* s.str. Such intergrading form could be found within both chromosomic types. Likewise, the two forms of *V. officinalis* described by Drabble (viz. forma *dentatifolia* Druce and forma *latifolia* Vahl) are represented both by tetraploids and octoploids. Druce's specimens of f. *dentatifolia* from Ashdown, Berks (Kew Herbarium), are putative tetraploids, and among the living plants of the same type both tetraploids (e.g. Pls. 170, 4, M. 2, 50; Pl. **7**, figs. 4, 7) and octoploids (Pls. 161, L. 3; Pl. **8**, fig. 8) have been found. These forms link up with gradually broader leaflets of f. *latifolia*. The majority of the herbarium specimens of the latter form represent putative octoploids; some corresponding types, however, have been found also among tetraploids (e.g. Pl. P. 14; Pl. **7**, fig. 4).

In general, in the various forms occurring within the collective species the characters are not regularly correlated; on the contrary, they appear in a variety of combinations. The species of Drabble's classification represent merely a few more or less distinct forms found within the polymorphic species together with many others. The distinct forms from the Cotswold Hills described by Dr Sprague presumably represent other combinations of characters. The numerous 'geographic species' of Kreyer (1930) seem to have the same value; the difficulty of a correct delimitation of these forms has been already emphasized by Sprague.

UNIFORMITY AND DIVERSITY WITHIN STRAINS

The observation of a number of strains in their natural habitats shows that, in general, locally occurring small groups of plants are morphologically uniform, and they seem to represent clones developed by vegetative reproduction of a single individual. On the other hand, groups of plants which extend over larger areas (along roadsides in dry valleys, on borders of woods and copses, along river banks) usually manifest some degree of morphological diversity. Such groups represent mixed populations developed from many seeds dispersed by the wind.

Examples of genic differences observed in such non-uniform strains are given for plants from Pinchley Wood (Cotswold Hills) grown at Kew (Table 8) and for the morphology of the leaf of a strain from Shewel Wood (Cotswold Hills) in its natural habitat (Table 9).

TABLE 8. *Morphology of a non-uniform strain from Pinchley Wood in garden culture*

	Sunny side of the road	Shady side of the road
Lateral leaflets:		
No. of pairs	6–7 or 10 pairs	6–8 pairs
Shape	Linear or narrowly lanceolate, sometimes strongly decurrent	Lanceolate, broadly lanceolate or ovate
Ratio width/length	0·134–0·180	0·170–0·275
Degree of toothing:		
Basiscopic margin	None, slight or distinct	None, slight or distinct
Acroscopic margin	None or slight	None or slight
Flowering stem:		
Height	50–105 cm.	40–95 cm.
General habit	Slender; erect or seldom prostrate	Robust; always erect
Degree of pubescence	Strong (4) or moderate (2)	Distinct (3) or moderate (2)
Presence of anthocyanin	Stems brownish green (2) or dark red (3)	Traces of anthocyanin (1) or stems brownish green (2)
Beginning of flowering	Early (5–12 June)	Early (5–12 June)

The strain from Pinchley Wood consisted of two different groups of tetraploid plants which in their natural habitat grew along the sunny and the shady side of the road (Herbarium specimens in Dr Sprague's collection, Kew Herbarium). Each group comprised a variety of forms, but on the average the plants on the shady side were more robust and had broader leaflets than those on the sunny side. Under conditions c cultivation the two groups in general retained the differences observed in nature (Pl. 7 fig. 4). It seems probable that in this mixed population different habitat preferences o the various forms favour a gradual topographic separation of two biotypes with a differen genic composition.

TABLE 9. *Morphology of the leaf of a non-uniform strain in nature. Shewel Wood*

Lateral leaflets:	
No. of pairs	5–10
Length	30–45 mm.
Shape	Linear, narrowly lanceolate to broadly lanceolate
Ratio width/length	0·13–0·30
Degree of toothing:	
Basiscopic margin	None, slight or distinct
Acroscopic margin	None or slight

In general, the tetraploid strains in the Cotswold Hills show a high degree of geni differentiation. A mixture of types occurs in Shewel Wood. The differences, summarize in Table 9, concern chiefly the shape of the leaflets and the number of pairs. A sti greater variety of forms has been described by Dr Sprague (p. 95) from a narrow, dry valle eastward from Lower Hilcot along the Withington Road (H.Sps. in Dr Sprague's collection Kew Herbarium). Some differences, e.g. the vigour and height of the flowering stem, ar induced by the environment and disappear in cultivation; others, however, are retaine and have presumably a genic basis (differences in the shape of the leaflets, ranging fro linear to broadly lanceolate (cp. Pl. 7, figs. 6, 7); in the toothing of the margins; in th number of lateral leaflets and in the presence of anthocyanin in the stem).

Likewise, a wide range of forms has been found by Dr Sprague in the Sapperton Valley In this valley the occurrence of the two polyploid types has been established by chromosom counts, the plants growing in a variety of habitats as separate colonies, presumably clone The comparison of the morphology of seven tetraploid clones from Sapperton in garde culture is summarized in Table 10 (cp. Pl. 7, fig. 4).

In conditions of cultivation each clone proved to be uniform, and differences betwee the clones appeared distinctly; they concerned the height of the stem, the degree o pubescence and the presence of anthocyanin, as well as the shape of the leaflets and th number of pairs, etc. In the different clones, these characters appear in various combi nations which might have arisen as the result of the Mendelian segregation of a hybrid

Some observations on the progeny raised from seeds of an octoploid plant prove tha sister plants may differ remarkably with regard to a number of characters. The mothe plant (Liv.Pl. 8) was a very robust octoploid found by Dr and Mrs Sprague and mysel in 1942 near Sapperton; it grew among *Glyceria* in the disused canal. Its seeds from ope pollination were germinated by me at Kew in 1943. The daughter plants flowered in 194 and showed distinct differences in respect to the shape of the leaflets and their numbe and, to some extent, in the height of the flowering stem, whereas other characters seeme to be true breeding (Table 11). The diversity within this sexual progeny presumabl results from Mendelian segregation and recombination, due to cross-pollination. Pl. 8 fig. 10 and Table 11 give some details of the morphology of three plants from this sexua offspring, and, in addition, of two separate octoploid clones from different habitats in th same locality. The following remarks may be added: plant 8/3 is similar to the mothe plant with regard to the shape of the leaflets; on the other hand plant 8/2 is remarkabl similar in this respect to plants of the clone M. 8, which represent the extreme *sambuc* *folia* type, whereas plant 8/1 has much smaller and narrower leaflets which link u with some forms represented on Pl. 8, fig. 8. The above observations throw light upo the origin of diversity in mixed populations which have the possibility of sexual repro duction. According to preliminary experiments carried out on plants at Kew, *V. officinali*

	Field no. of clones						
	M. 1	M. 2	M. 3	M. 4	M. 5	M. 6	M. 7
Lateral leaflets:							
No. of pairs	6	6–8	7–9	5–7	5	5–6	7–9
Shape	Linear	Narrowly lanceolate	Linear	Narrowly lanceolate	Lanceolate	Narrowly lanceolate	Lanceolate
Ratio width/length	0·13	0·20	0·13	0·17	0·236	0·20	0·21
Degree of toothing:							
Basiscopic margin	Very slight	Strong	None	Very slight	None	Distinct	Strong
Acroscopic margin	None or very slight	Strong	None	None or very slight	None	Very slight	Variable
Flowering stem:	Slender	Slender	Robust	Slender	Slender	Very slender	Very robust
Height (cm.)	75–82	75–90	65–75	84–90	65–80	100–118	100–104
Degree of pubescence	Distinct (3)	Distinct (3)	Strong (4)	Moderate (2)	Moderate (2)	Moderate (2)	Strong (4)
Presence of anthocyanin	(3)	(0)	(1)	(2)	(2)	(1)	(3)
Colour of the flowers	Pink	Almost white	Almost white	Pale pink	Pale pink	Almost white	Dark pink
Beginning of flowering	5–10 June	1–10 June	30 May–5 June	30 May–10 June	5 June	12 June	5 June

Table 11. *Octoploids from Sapperton grown at Kew*

Field nos. of the plants...	Sister plants from seeds			Clone 6 (=V. 155 Spr.)	Clone M. 8
	8/3	8/1	8/2		
Lateral leaflets:					
No. of pairs	6	3	3	4–5	4
Size	Medium	Medium	Very large	Very large	Very large
Shape	Ovate	Lanceolate	Ovate	Lanceolate	Ovate
Ratio width/length	0·46	0·25	0·32	0·23	0·33
Degree of toothing:					
Basiscopic margin	A few teeth irregular in shape and distribution	Numerous small teeth	Strong toothing, large teeth	Strong toothing, large teeth	Very strong toothing, very large teeth
Acroscopic margin	Slight toothing of the same type	As above	Same type, less strong	Same type, less strong	Same type, less strong
Flowering stem:					
Height (cm.)	95	95	125	130–165	170–180
Degree of pubescence	Slight (1)	Slight (1)	Slight (1)	Slight (1)	Moderate (2)
Anthocyanin	(0)	(0)	(0)	(1)	(1)
Beginning of flowering	28 June	4 July	27 June	28 June–4 July	28 June–1 July

seems to be strongly allogamous. This must lead inevitably to a high degree of heterozygosity, repeated cross-pollinations giving rise to new combinations followed by segregation in sexual progenies. On the other hand, the uniformity observed in some smalle isolated groups of plants is caused by the vegetative propagation.

Self-pollination and cross-experiments

In 1944 and 1945 some experiments were carried out with selfing and crossing of the tw polyploid types. Self-pollination of two tetraploid plants and four octoploid plants representing various morphological types, gave in the two successive seasons entirel negative results. Cross-experiments between the two chromosomic types which wer undertaken on a small scale in the same seasons aimed at the production of a hexaploi type with 42 chromosomes, hitherto unknown in the Valerians. In the majority of th crosses, the octoploids were used as mother plants. In 1944 extremely different morphological types were selected for these crosses: *sambucifolia* as the mother plants and tetraploids with nearly linear leaflets as the pollen parents. In view of the entirely negativ results, in 1945 octoploids with narrow leaflets and slender stems were crossed to vigorou tetraploids. However, most of these crosses also failed; only in a few instances did th embryos begin their development, but these died subsequently at early stages.

In nature, there is very little probability of a spontaneous intercrossing of the tw chromosomic types, in view of the fact that the tetraploids and the octoploids usuall occupy different habitats. In rare instances when their areas are not sharply delimited the existing barrier of incompatibility prevents the formation of the hexaploid type i nature.

Vegetative propagation

The method of vegetative reproduction by stolons (soboles) has been described in detai by Dr Sprague (1943), and only a few additional observations are required here. Study of a large number of living specimens belonging to the two polyploid types and representing a wide range of forms shows that vegetative reproduction by stolons may occu in all forms and irrespective of the number of chromosomes. External conditions may favour the development of the stolons or, on the contrary, they may restrict their formation. The extreme *sambucifolia* plants usually develop abundantly long stolons, both in nature and in garden culture. In other types, both octoploid and tetraploid, there are sometimes distinct differences in the capacity of vegetative propagation; they cannot, however, be correlated with a definite morphological type. Among tetraploids in the Cotswolds vigorous plants, approaching more or less the *officinalis* type, developed long stolons, the same plants in culture behaving in the same way. Some plants with linear leaflets, approaching the extreme *angustifolia* type, in their natural habitats did not show a well-marked tendency to form stolons; in garden culture, however, the production of stolons was very intense. One of the plants from Shewel Wood, in nature of moderate performance (Liv.Pl. T. 11), in culture each year developed a large number of long stolons and showed a tendency to rapid expansion in the same degree as did *sambucifolia* plants. Another plant from the same locality, a form with broader leaflets (Liv.Pl. T. 10), had a much poorer development in garden culture, and after two years only a few young plants were produced by vegetative propagation. It is noteworthy that some plants which in natural habitats are stunted and unable to flower may exhibit under conditions of cultivation a greatly increased capacity of vegetative reproduction. This behaviour was observed on a number of tetraploid clones from the Wiltshire Downs and from Birdlip, Cotswold Hills (coll. Dr W. O. James); the latter clone (Liv.Pl. 170) was native on an open limestone scree. In 1943 two plants only were planted at Kew; in garden culture these plants started an intense development and growth, and each year a considerable numbe of stolons gave rise to new rosettes. In 1945 the total number of flowering stems amounted to 34; they were surrounded by many young rosettes whose flowering was expected i

1946. In nature, this capacity of a rapid expansion by vegetative propagation is limited by the environment.

As already mentioned, in *V. officinalis* cross-pollination followed by segregation leads to the production of a great number of forms representing, within each chromosomic type, various combinations of genes. Vegetative reproduction plays an important part in the fixation of these forms, since in this way a single plant gives rise to a clone; a uniform group of plants which may gradually extend its area. Owing to self-sterility, isolated colonies are unable to produce seeds and are confined to vegetative propagation. In this way each combination of genes resulting from sexual reproduction may be fixed, in spite of its heterozygosity.

Transplant experiments

The cultivation of plants brought from their natural habitats to the garden made it possible to draw conclusions with regard to differences in the genetic structure of the various strains, and also to compare the development of the same clones in nature and in garden culture and to study the extent of the phenotypic variability within a single clone. On the whole, *V. officinalis* has a high degree of phenotypic plasticity, chiefly expressed in the height of the flowering stem and the size of the leaflets. The changes induced by transplanting seem to be purely quantitative; they may, however, strongly affect the phenotype of the plants. Nevertheless despite the variability in size, the shape of the leaflets is only slightly affected, and the distinct features of the plants are retained under conditions of cultivation. The modifications induced in the various clones in garden culture are not always parallel; they merely result from the differences existing between the conditions in native habitats and in cultivation, and therefore the changes may go in opposite directions after transplanting, resulting in increase or decrease of size and vigour. For example, some plants native in extremely dry and exposed habitats increase their vigour in garden culture; others, transplanted from moist and rich soils, develop shorter stems and smaller leaflets than in nature (Table 12 and Pl. 7, fig. 5).

TABLE 12. *Height of the stems of ten clones from the Cotswolds in nature and culture*

Field no. of clones	Height of the flowering stems		Localities and habitat of the clones
	Natural habitat	Garden culture	
Tetraploids:			
T. 3	0 (no flowering in nature)	40–50 cm.	Slope above Chatcombe Wood. Inf. Oolite grassland
T. 4	135 cm. (very robust stem)	60–80 cm.	Chatcombe Wood. Border of the wood
T. 6	13–17 cm. (dwarf plants)	33–55 cm.	Between Pinchley Wood and Pegglesworth. Dry pasture
T. 7	150 cm. (very vigorous)	50–75 cm.	Withington Road. Woody slope above the shady side of the road
T. 10	95 cm. (moderate performance)	90 cm.	Shewel Wood, near the stream
T. 11	75–80 cm. (moderate performance)	90–100 cm. (very robust)	Shewel Wood, under *Corylus*
Octoploids:			
T. 8	150 cm.	85 cm.	River Churn at Cliffۥerdine riverside
T. 9	160 cm.	55 cm.	Roadside bank, among long grass between Marsden and Colesbourne
M. 8	195 cm. (extremely vigorous)	170–180 cm.	Sapperton Valley, near the disused canal
6	180 cm. (extremely vigorous)	150–165 cm.	Sapperton Valley, marshy ground

For the octoploids the differences in the external conditions of the native habitats and of garden culture are less marked than for the tetraploids, and consequently the changes after transplanting are not so distinct. Examples of extreme modifications of the size of the leaflets of tetraploids in culture, as compared with their development in nature, are given (Pl. 7, fig. 5). The difference in size is striking, but the shape remains approximately the same. On the contrary, the leaflets of the octoploids show only slight size differences (cp. Pl. 8, fig. 8; Liv.Pls. T. 8, T. 12, T. 16, leaflets from nature and culture), and some extremely vigorous octoploids (clones M. 8 and 6) are similar in their development in their natural habitats and in conditions of cultivation.

GEOGRAPHICAL DISTRIBUTION OF THE TWO TYPES

The tetraploids seem to be confined to south England and parts of the Midlands, whereas the octoploids extend from the south of England to the north of Scotland. Although the areas of the two types overlap, the plants occupy different habitats and are thus separated ecologically.

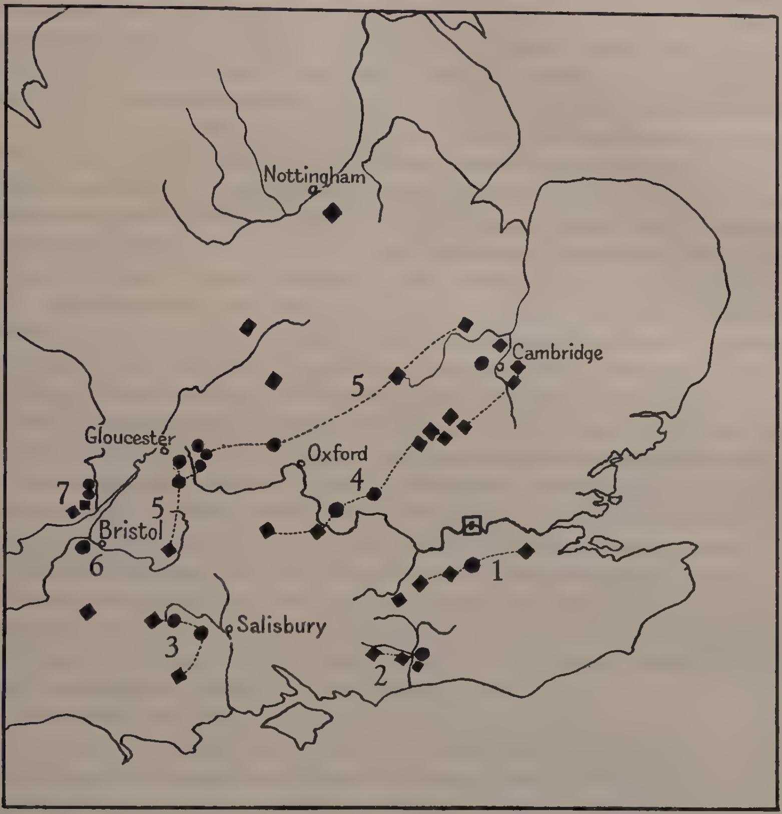
The distribution of the tetraploids roughly corresponds to that of plants which, according to Matthews (1937) and to Salisbury (1932), represent in the British flora the continental southern geographic element. The corresponding type on the European continent, *V. angustifolia* Host, is not quite identical with any of the tetraploid forms from Great Britain, as already observed by Sprague (p. 93) from a study of herbarium specimens. However, a regional differentiation may be presumed within a species in groups of plants which develop in quite different climatic conditions. Pollen examination of the herbarium specimen mentioned by Sprague (*Fl. Exsicc. Austr.-Hung.* no. 3445, Kew Herb.) indicates that this plant is a tetraploid (mean = 45·75), and this detail seems to be important in connexion with the problem of origin of the British tetraploid Valerians.

In England, the northern limit of the tetraploid area is diagonal; it runs from south-west to north-east and roughly corresponds to the line connecting the Bristol Channel and the Wash. Only a few putative tetraploids have been found among the herbarium specimens from localities situated northwards of this line (Warwick and Nottingham); these records, however, require confirmation by chromosome counts on living plants. It is possible that additional records may slightly alter the area of the tetraploids, but it seems, however, that they will not substantially affect its general outline.

Within the area occupied by the tetraploids, their occurrence is restricted to relatively dry habitats. This suggests that this type is less hardy than the higher polyploids which extend over a much larger area and are able to survive in a variety of external conditions.

Presumably the northern and western expansion of the tetraploids is prevented by a climatic barrier in the same way as the distribution of a number of species belonging to the continental southern element of the British flora (cp. Matthews, 1937, p. 39) is limited. Other factors which should be taken into consideration are the edaphic conditions and the topography of the terrain, as well as the plant community.

Within the area of distribution, the tetraploids occur in hilly regions, on slopes and escarpments, as well as in dry valleys. Their distribution seems to follow definite geological formations, and can be traced along the following main lines: (1) On Chalk: North Downs, South Downs, South Wiltshire Downs to Somerset borders (westwards) and Dorset (south-westwards); downs in Berkshire, Chiltern Hills, Hertfordshire, south Cambridgeshire. (2) On Oolite: Cotswold Hills, north Wiltshire and Oxon, as well as the extension of the area towards Lincoln. (3) On Carboniferous limestone (isolated areas): Wye Valley, Avon Valley below Bristol. (4) Calcareous boulder clay near Cambridge. In addition to the above formations, some putative tetraploids seem to occur very locally also on the Lias limestone (map of distribution, Text-fig. 3). In view of the fact that the tetraploids represent a xerophilous type, it is possible that the calcareous soils are suitable for these plants owing to their physical features (good drainage) rather than their chemical composition; but another possibility, that of the preference for soils with a higher pH value, as well as a suitable plant community, should also be taken into consideration. On the other hand, the octoploids may find favourable conditions in swampy soils with a higher acidity (sedgemoors). Within the area of the tetraploids they are ecologically distinctly separated from the latter type, occurring either in a low country, or in hilly regions at lower altitudes and in moister soil than the tetraploids. Beyond the tetraploid area, however, the octoploids are not limited to the above habitats. Besides their typical occurrence along river banks, ditch banks and in bogs, as well as along margins of woods and road sides, they are able to exist also in much drier places. Sometimes they grow at higher altitudes, on dry steep slopes, and they have been found growing even in cracks of solid limestone rocks (Cheddar Gorge). Thus, beyond the common area, the octoploids are represented by both hygrophilous and xerophilous forms, and in the north and west they are able to survive in habitats corresponding with those occupied by the tetraploids in the south and east.



Text-fig. 3. Map of distribution of the tetraploid Valerians. 1, 2, 3, 4, main centres in the Chalk area: 1, North Downs; 2, South Downs; 3, Downs of south Wiltshire and Dorset; 4, the Chalk area ranging from Berkshire to south Cambridgeshire. 5, the area of Oolitic limestone, with its main centre in the Cotswold Hills. 6, 7, two isolated areas on Carboniferous limestone: 6, Avon Valley; 7, Wye Valley; in addition, a few scattered localities on Lias and Keuper. Black circles represent localities in which living plants have been collected for cytological investigations; black squares represent localities from which herbarium specimens identified as tetraploids have been studied.

Discussion

The present study represents a new attempt to analyse the problem of diversity in the polymorphic species *V. officinalis* Linn. The very great plasticity of *Valeriana* in different habitats in nature renders extremely difficult the correct estimation of the genotypic diversity. Therefore, although the results of the present study have thrown some light upon this difficult problem, further study is still required.

Cytological investigations and the cultivation of a large material from a variety of habitats in nature in uniform conditions have proved that the genetical basis of the morphological diversity in *Valeriana* is twofold: there exists a polyploid differentiation within the British Valerians, and, in addition, each chromosomic type shows a high degree of genic differentiation. A polyploid differentiation of Valerians of the European continent has been found by Senjaninova (1927), as well as by Meurman (1925) and by Runquist (1937), whereas, for Great Britain, the higher polyploid, viz. the octoploid with 56 chromosomes, has been reported by Todd (1942) as the only type. In addition to that type, the occurrence of the presumably older form, the tetraploid with 28 somatic chromosomes, has been established in the course of the present work.

The genic differentiation within each type concerns a great number of characters of the leaves and the flowering stem. The morphological analysis of a number of strains from nature has shown that these characters are not regularly correlated, but, on the contrary, they appear in a variety of combinations. In view of this, any attempt to subdivide this polymorphic species into smaller units on a morphological basis must result in a failure. A limited number of distinct forms described by Drabble (1932) as separate species (or forms) occur within the collective species together with many intermediates which represent presumably different combinations of independently transmitted genes.

The various forms arise from sexual reproduction. Experiments in selfing of some plants representing the two chromosomic types have shown a high degree of self-sterility. Repeated cross-pollination within each polyploid type leads to a high degree of heterozygosity and sexual propagation gives rise to many new forms, resulting from Mendelian segregation and recombination. Vegetative reproduction plays an important part in the fixation of these heterozygous forms, since a single plant gives rise to a clone. In such a uniform group of plants which represent strictly the same genotype, a further genic differentiation may depend only on somatic mutations (cp. Darlington, 1940). In populations exhibiting genic differentiation the various forms may show some habitat preferences. If they occur at the limit of two different habitats, a gradual topographic separation of two biotypes with a different genic composition may take place. Presumably, such a process is at work in the mixed population at Pinchley Wood, Glos., where different external factors seem to favour a selection in two opposite ways.

Concerning the study of the morphology of the various types it should be added that further investigations based on the examination of sexual progenies are required. In view of the self-sterility, various types of crosses should be undertaken with the object of studying the Mendelian inheritance of some genes. Another line of research could throw some light upon the difference in the genetic effect of four or eight sets of an identical genic structure in tetraploids and octoploids, and the method of experimental doubling of chromosomes could be applied for the study of the interrelation of the corresponding forms of the two polyploid series. In the light of such results, the correctness of the above-presented assumption concerning the origin of some extreme octoploid forms with narrow leaflets could be tested.

Distinct differences in the distribution of the two polyploid types have been established on the basis of field work, combined with cytological examination of the living specimens, and with special herbarium studies. The tetraploids have a much smaller area of distribution than the octoploids; they seem to be limited to the southern counties and parts of the Midlands, whereas the area of the octoploids extends from the southern counties to the north of Scotland. Within the common area, the tetraploids are confined to particular habitats, and on the whole they represent xerophilous forms, growing in relatively dry soils, in hilly regions, on slopes and in dry valleys. Their distribution seems to follow some definite geological formations, their occurrence being traced along the following main lines: on Chalk along the North Downs, some parts of the South Downs, south Wiltshire Downs, and along the Chalk area extending from Berkshire to south Cambridgeshire; on Oolitic limestone, with its main centre in the Cotswold Hills; as well as in some isolated areas of the Carboniferous limestone (cp. map of distribution, Text-fig. 3). In their general area of distribution, the tetraploids roughly correspond to plants representing in the British flora the continental southern geographic element, as described by Matthews (1937) and by Salisbury (1932). Although the corresponding type of the European continent, *V. angustifolia* Host, is not quite identical with any of the tetraploid forms from Great Britain, a regional differentiation may exist here.

Differences in the areas of distribution of types with lower and higher chromosome numbers have been found by some authors. Hagerup was the first to show that the area of distribution of a species may be extended as a result of polyploidy. In his studies on desert plants (1932) he established that the polyploid types are more vigorous and more resistant than the respective diploids, and that therefore they are able to advance to some unfavourable habitats, inaccessible to diploids. In a later paper (1939), he gave a comparison of the areas and habitats of a diploid and tetraploid species of *Deschampsia*. The only diploid species within this genus is *D. setacea* ($n=7$), which is very exclusive in the selection of its habitats, and consequently has a very small ecological range. On the other hand, in *D. flexuosa* ($n=14$), tetraploidy is accompanied by an immense increase of the ecological and geographical range. The same is true for the American species of *Tradescantia*, allied to *T. virginiana* (Anderson & Sax, 1936; Anderson & Woodson, 1935). In this genus, likewise, the diploid species are of limited distribution and usually they are restricted to some particular habitats. By contrast, the tetraploids have a wide distribution; they are hardier than the diploids and are able to flourish in a variety of habitats. In the above examples the occurrence of polyploidy has greatly extended the range of the respective genera. Similarly, the diploid and hexaploid types within the collective species *Potentilla argentea* L. show differences in their distribution, as observed by A. & G. Müntzing (1941). The diploids have a more northern distribution than the hexaploids, the former representing apomictic diploid biotypes native in Scandinavia, whereas the latter also grow in central Europe. Details of the distribution of biotypes with different numbers of chromosomes give some indication concerning the direction of the advance to new areas, resulting from the doubling of genomes.

In *Valeriana*, the tetraploids, which represent the phylogenetically older form, have presumably spread northwards from the European continent to the south of Great Britain, as well as to parts of the Midlands, where they were able to establish themselves as members of some plant communities. Presumably, however, a climatic barrier has prevented their further advance northwards. By contrast, the presumably younger type, the octoploids, were able to advance beyond this area. Within their area the tetraploids are restricted to some particular habitats, and in some localities the external conditions seem to be very favourable for their development, as in the Cotswolds. Some other parts of the area, however, are definitely less favourable, probably not with regard to edaphic conditions, but rather in view of their inability to compete with other species in plant communities. They seem to survive chiefly in situations in which the competition is not too strong, and this is probably the reason for their very local occurrence in some habitats. In some seral communities they are distinctly in the state of regression, as, for instance, in some localities in the Chilterns (High Wycombe) and on the North Downs (Caterham). According to Tansley (1939, p. 227), in a seral community, earlier members may be suppressed by later ones, and this leads to the normal succession. In this process of the gradual elimination of the tetraploid *Valeriana* competition seems to represent the most important factor, and probably limits the vertical distribution of the tetraploids which are confined chiefly to slopes, escarpments and dry valleys. In general they are able to persist only in habitats with no abundant and tall vegetation. The problem arises whether the Valerians are still existing in some of the localities where older herbarium specimens have been collected. It seems rather probable that at least in some habitats they have already perished in accordance with the general laws of development of plant communities. The role of competition in the elimination of the tetraploids could be observed to some extent in garden culture at Kew, as a part of the bed has been left in the summer of 1945 without weeding. In such conditions, the plants, which were strongly overgrown by long grass and tall weeds, were greatly weakened and some have perished. Presumably in the same way in nature the tetraploids are unable to establish themselves on lower altitudes in habitats which are favourable for the development of other genera, and are therefore confined to less favourable situations in which the competition is not too strong. On the other hand, the octoploids which occur on moister soil in a variety of habitats seem to be much more resistant with regard to competition, and they were able to extend notably the geographical and ecological range of the species.

Presumably in consequence of the chromosome doubling followed by their advance to new areas which are inaccessible to tetraploids, new possibilities with regard to hybridization with related species have been created. As pointed out by Darlington (1940), in this way the distribution of higher polyploids may overlap areas of some related species, but owing to the increase of the number of chromosomes, the barrier of incompatibility may be upset. In *Valeriana*, the giant plants of the extreme *sambucifolia* type might be regarded as a related species, or at least a separate group. However, as already mentioned, these extreme forms are connected with the other octoploids by a range of intermediates, the latter having possibly arisen from crosses followed by Mendelian segregation. Some observations on the sexual progeny of an extreme plant have shown the diversity resulting from the segregation of a heterozygote (cp. Table 11 and Pl. 8, fig. 10). In view of the occurrence of permanently hybrid clones representing a range of intermediate forms between the extreme *sambucifolia* and plants roughly corresponding to *V. officinalis* s.str., the separation of these forms is practically impossible. It seems reasonable to assume that a kind of fusion has taken place between two formerly separate groups, the octoploid *sambucifolia* and the octoploid forms of *officinalis*, and these are linked by a great number of hybrid forms, well established in a variety of habitats. The narrower range of diversity in tetraploid forms is presumably due to the fact that, owing to the ecological separation and the barrier of incompatibility between the two chromosomic types, the exchange of genes is limited to crosses within this group. In addition, the very local occurrence of the tetraploids in some habitats does not favour intercrossing. Therefore, the presumed fusion of *sambucifolia* with *officinalis* has been achieved exclusively on the octoploid level. It resulted in the production of a so-called 'hybrid swarm' as described in the New Zealand flora by Allan (1940). According to Huxley (1942), where some of the products of initial hybridization continue to cross, elaborate complexes are produced in which a number of initial forms are combined in an evolutionary reticulum (p. 147). In view of the fact that the tetraploid Valerians are being left outside this process of fusion and of repeated intercrossing, the problem arises concerning the position of this group in the collective species *V. officinalis* sensu lato. In this respect, a great difficulty is created by the fact that purely morphological criteria are inadequate for a correct estimation of the chromosomic type. The geographic distribution and ecology, distinctly different in tetraploids and octoploids, might suggest the delimitation of the tetraploids as a climatic race. Sometimes, however, the octoploids are indistinguishable from tetraploids, and therefore such a subdivision would be valueless for a taxonomist. By contrast with some other polymorphic species, in *Valeriana* it is impossible to distinguish, within each chromosomic type, a few well-defined climatic races such as those occurring in *Potentilla glandulosa* Lindl. in California, as well as in the *Achillea millefolium* complex (*A. borealis* Bong., $n=27$, and *A. lanulosa* Nutt., $n=18$), described by Clausen, Keck & Hiesey (1941, 1942). In *Valeriana* the differentiation has brought about the existence of a great number of forms (heterozygous clones) which should be rather considered as climatic biotypes, or as ecotypes confined to some particular habitats. Corresponding forms, however, of such types have been found in the two chromosomic groups: chalk or limestone forms in the south are tetraploid, whereas in the north they are replaced by similar octoploid limestone forms. This suggests that, as pointed out by Sprague (1944), 'the change from the tetraploid to the octoploid condition had taken place not once but in many instances, and that the tetraploid and octoploid sets of plants represent not two separate taxonomic groups, but rather two evolutionary stages of one and the same series of taxonomic forms'. Such corresponding forms are presumably of common origin, and the higher polyploid was formed in the way of somatic chromosome doubling. On the other hand, octoploid forms which have no corresponding tetraploid type have presumably a different origin and belong to the 'hybrid swarm' linking up *officinalis* with *sambucifolia*.

Thus, apart from some smaller changes due to gene mutations, presumably two different major mechanisms were at work in creating the wide range of forms which represent the polymorphic species *V. officinalis* Linn. sensu lato: the doubling of chromosomes and the intercrossing of the newly produced higher polyploids with giant octoploid *sambucifolia* plants.

SUMMARY

The considerable range of forms within the collective species *Valeriana officinalis* Linn. sensu lato is due to three main causes: (*a*) a high degree of phenotypic plasticity in natural habitats; (*b*) a polyploid differentiation with tetraploids ($2n=28$), representing the presumably older types, and octoploids ($2n=56$) representing the younger type; (*c*) a distinct genic differentiation within each chromosomic group, which brings about a considerable number of forms with more or less distinct morphological differences.

A detailed morphological analysis of a number of characters in the various forms has shown that purely morphological criteria are inadequate for the delimitation of the two polyploids which are connected by a range of intergrading forms. The various characters are not regularly correlated in the strains occurring in nature; on the contrary, they appear in a variety of combinations. In view of this, any attempt to subdivide the polymorphic species into smaller units must fail.

The various forms are produced by sexual reproduction. Repeated cross-pollination is followed by Mendelian segregation and recombination, while vegetative propagation contributes to the fixation of the numerous heterozygous forms. The two polyploids are intersterile.

Distinct differences occur in the distribution of the two polyploids. The area of the tetraploids is much smaller than that of the octoploids. The former is limited to the south of England and parts of the Midlands, the latter extends from the south of England to the north of Scotland. Within the common area, the tetraploids are confined to particular dry habitats in hilly regions and are ecologically separated from the octoploids which grow at lower altitudes in moist soil. In their distribution the tetraploids follow some definite geological formations, chiefly Chalk, Oolitic limestone, as well as some areas of Carboniferous limestone in the south-west. The general area roughly corresponds to that of plants representing in the British flora the continental southern geographic element. The spreading northwards of the tetraploids seems to be prevented by a climatic barrier, and in contrast, the octoploids were able to advance beyond this area and to extend notably the geographical and ecological range of the species.

The remarkably wider range of forms of the octoploids is possibly due to their crossing with the extreme *sambucifolia* plants followed by segregation and recombination. On the other hand, in the tetraploids the narrower range of forms is presumably due to the ecological separation and the barrier of incompatibility which in the tetraploids limits the exchange of genes to crosses within this group. Therefore, the process of partial fusion with the *sambucifolia* type has been achieved exclusively on the octoploid level.

In the formation of the wide range of forms within the collective species *V. officinalis* Linn. sensu lato, presumably two different major mechanisms were at work: the doubling of chromosomes and the intercrossing of the newly produced higher polyploids with closely related plants belonging to the *sambucifolia* type.

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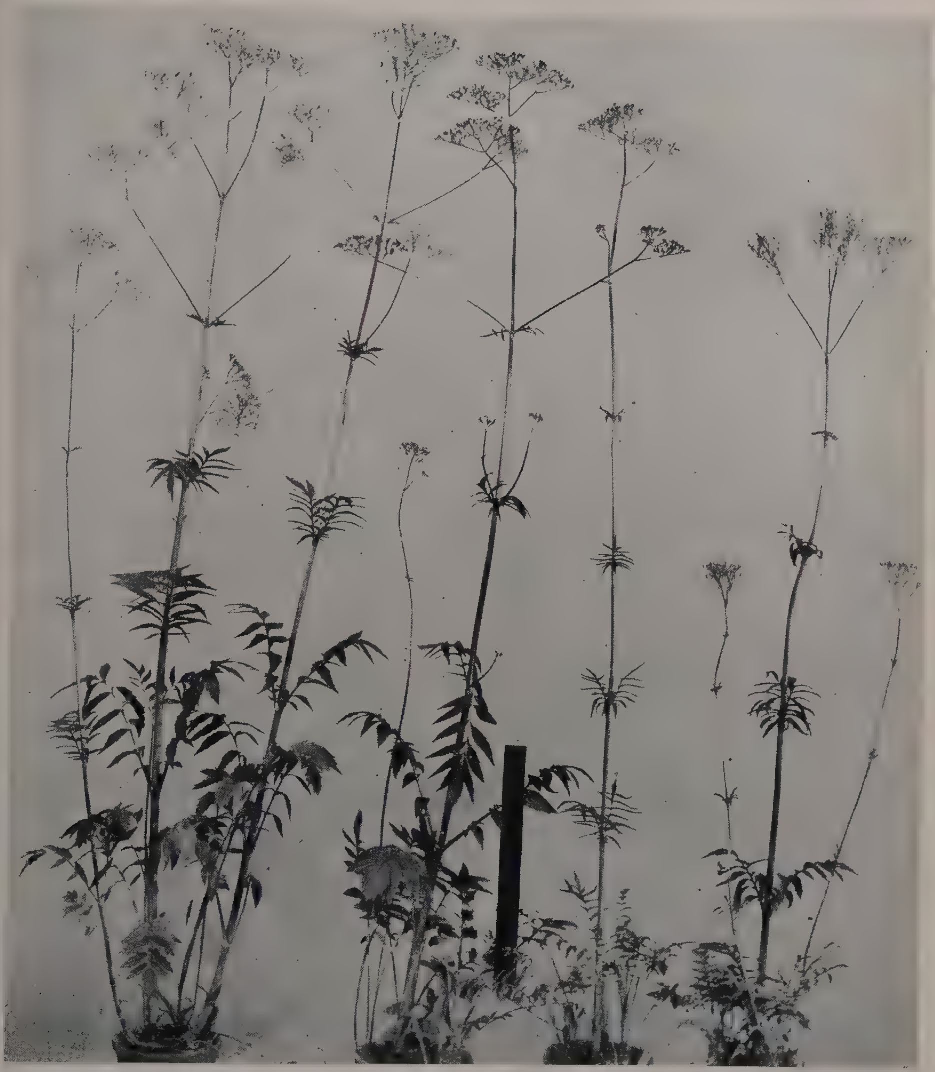

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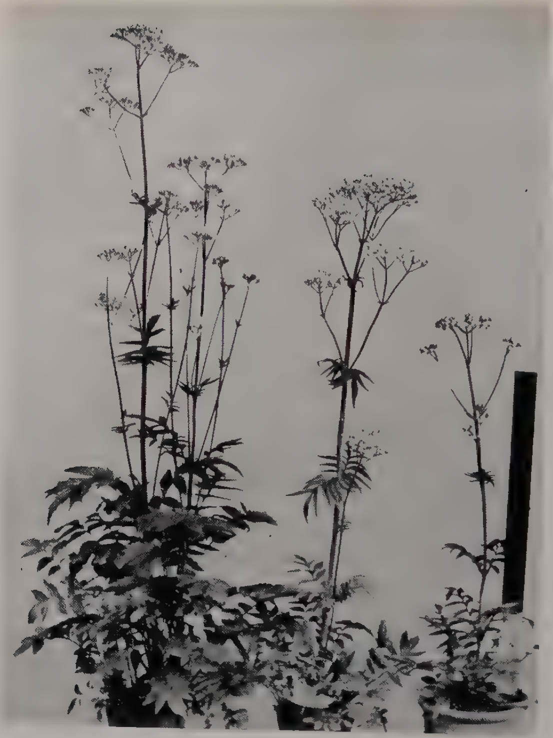

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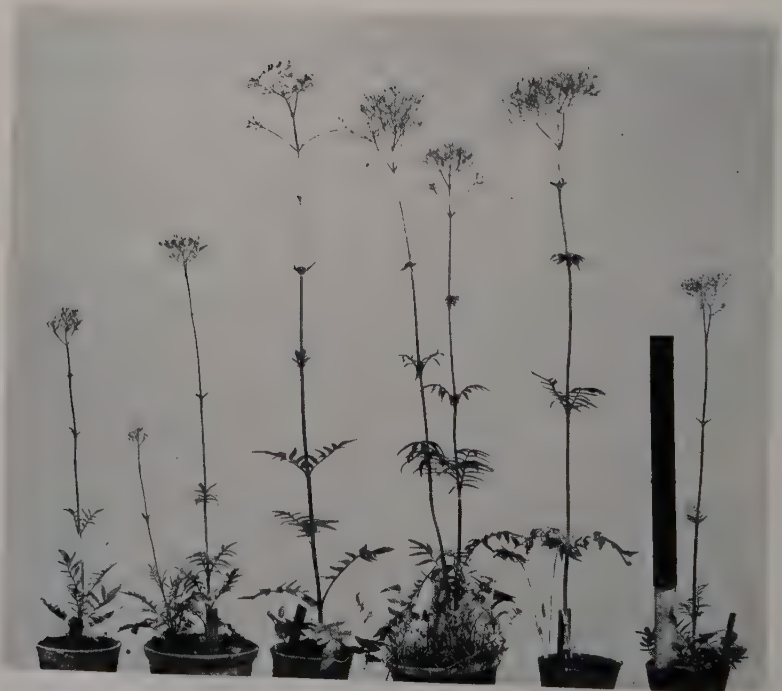

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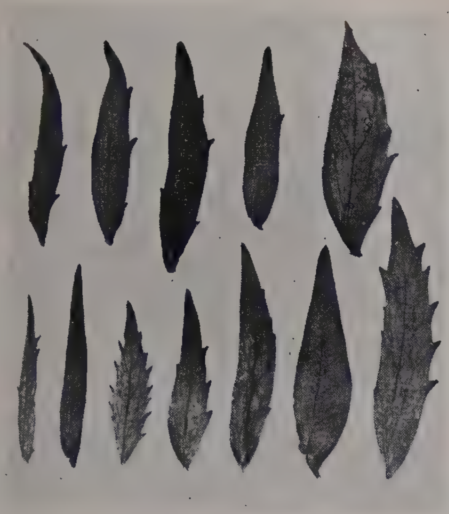

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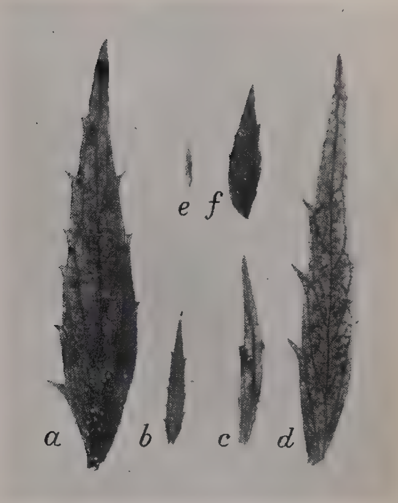

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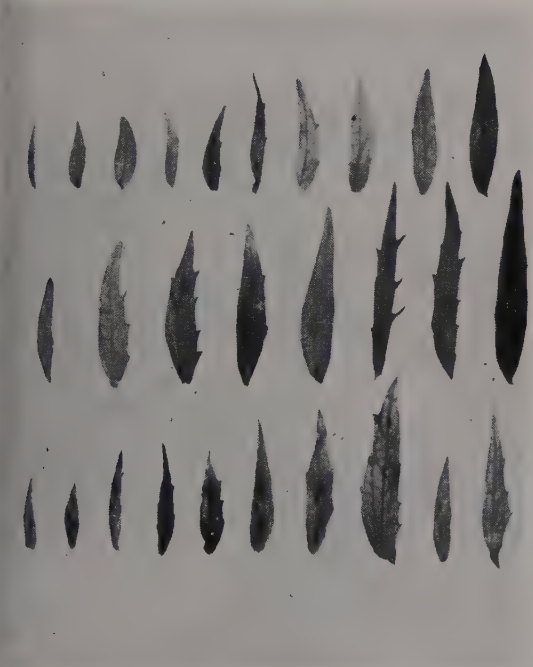

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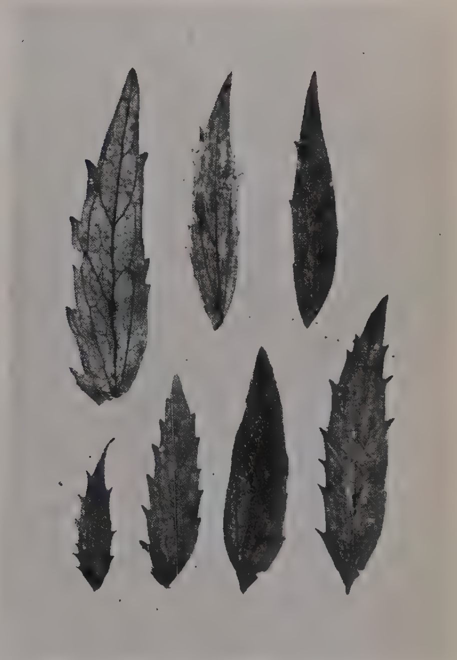

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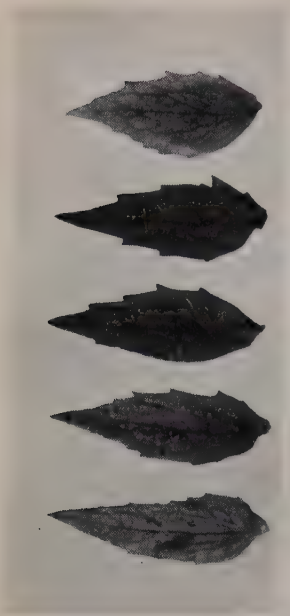

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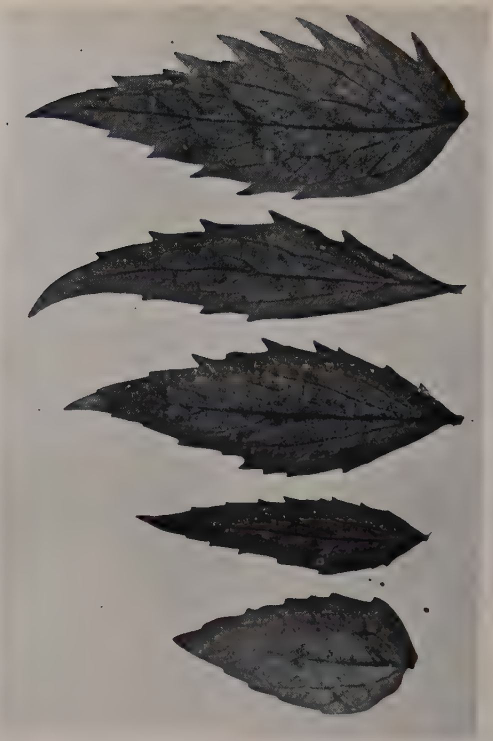

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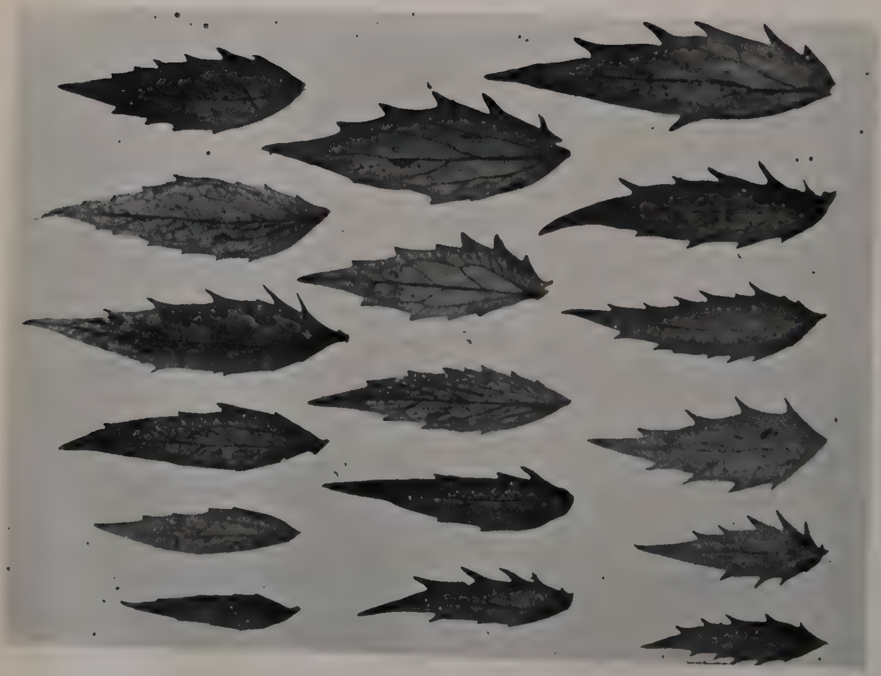


Fig. 8.

EXPLANATION OF PLATES

Plates 5 and 6

Photos of plants grown at Kew

Fig. 1. Four tall plants. From left to right: an octoploid (plant L. 8) from marshy ground by river Churn, near Colesbourne, Glos.; an octoploid (plant K. 3) from Chescombe Wood, Glos.; a slender tetraploid (plant M. 6) from Sapperton, Glos.; a vigorous tetraploid (plant M. 7) from Sapperton.

Fig. 2. Three short vigorous plants. From left to right: an octoploid (plant N. 8) from Tavistock, south Devon; a short robust tetraploid (plant P. 7) from Pinchley Wood (shady side of the road), Glos.; a short octoploid (plant 108) from Mayfield, Staffs. The tetraploid P. 7 is intermediate in height and vigour between the two octoploids.

Fig. 3. Six slender plants. On the left, three octoploids: plant 24 from Llandovery, Carmarthen, Wales; plant 19 from Aberdeen; plant 17, a rather small plant, from bank of the Thames-Severn Canal, Glos. On the right, three tetraploids: plant 69 from Chiltern Hills, near Kingston Wood, Oxon; plant T. 7 from a woody slope above Withington Road, Glos.; plant T. 3 from a dry pasture above Chatcombe Wood, Glos. The slender octoploids are similar to tetraploids. (The black ruler is 1 ft. long.)

Plates 7 and 8

Photos of lateral leaflets of stem leaves showing the wide range of diversity. The number of lateral leaflets in the respective compound leaves is given in brackets.

Fig. 4. Above: leaflets of five plants of a mixed tetraploid population at Pinchley Wood, Glos. (cp. Table 8). From left to right: sunny side of the road, plant O. 1 (7 prs.); plant O. 9 (10 prs.); shady side of the road: plant P. 6 (7 prs.); plant P. 2 (8 prs.); plant P. 14 (7 prs.). Below: leaflets of seven plants representing separate tetraploid clones from Sapperton, Glos. (cp. Table 10). From left to right: plant M. 1 (6 prs.); plant M. 3 (7–9 prs.); plant M. 2 (9–10 prs.); plant M. 6 (6 prs.); plant M. 4 (9 prs.); plant M. 5 (5 prs.); plant 7 (7–9 prs.). In all leaflets the basiscopic margin is to the right. All plants from garden culture at Kew. (×0·55.)

Fig. 5. Comparison of the development of the leaflets in natural habitats and in conditions of cultivation in three tetraploid plants. Plant T. 7 (a vigorous tetraploid from a woody slope above Withington Road): *a*, from nature; *b*, from culture; plant T. 11 (Shewel Wood, Glos.): *c*, from nature; *d*, from culture; plant T. 6 (from a dry pasture between Pinchley Wood and Pegglesworth): *e*, from nature (a dwarfed flowering plant); *f*, from culture. In all leaflets the basiscopic margin is to the left. (×0·66.)

Fig. 6. Small and narrow leaflets of tetraploids and octoploids. First row, tetraploids from natural habitats (from left to right): plant 117*b* from Caterham, North Downs (7 prs.); plant 143 from Avon Valley (7 prs.); plant T. 2 from Chatcombe Wood, Glos. (9–10 prs.); plant 5 from Withington Road, Glos. (6 prs.); H.Sp. 108 from Colerne, north Wilts. (7 prs.); plant 112 from Wyndcliff, Mon. (9 prs.); plant 126 from High Wycombe, Bucks. (6 prs.); plant 142 from Avon Valley, Som. (6 prs.); plant 130 from Amberley, South Downs (7–8 prs.); plant T. 11*a* from Shewel, Glos. (7–8 prs.). Second row, tetraploids grown at Kew: plant J from Withington Road (6–7 prs.); plant 69 from Kingston Wood, Chiltern Hills (6–7 prs.); plant 28 from Wiltshire Downs (6–7 prs.); plant 26 from Hailey Wood, Cambridge (7–8 prs.); plant T. 3 from Chatcombe Wood, Glos. (9–10 prs.); plant M. 1 from Sapperton (6 prs.); plant T. 5 from Chatcombe Wood (6 prs.); plant M. 3 from Sapperton, Glos. (7–9 prs.). Third row, eight octoploids from natural habitats and two octoploids grown at Kew: plant 141 from Cheddar Gorge (6 prs.); H.Sp. 107 from Fort William, west Inverness (5 prs.); plant 136 from Cheddar Gorge (8–9 prs.); H.Sp. 107*a* from Fort William, west Inverness (6 prs.); plant 122 from Combs, Pennines (6 prs.); plants 137 (6 prs.), 134 (5 prs.) and 131 (6–8 prs.) from Cheddar Gorge. Two plants grown at Kew: plant 24 from Llandovery, Wales (5 prs.); plant 103 from Corfe Castle, Dorset (5 prs.). In all leaflets the basiscopic margin is to the right. All the above plants have been investigated cytologically, except the H.Sps. from north Wilts and from west Inverness. The chromosomic type of these three plants has been estimated from pollen measurements. (×0·55.)

Fig. 7. Large and relatively broad leaflets of tetraploids from nature (above) and from culture (below). First row: plant T. 4, the largest tetraploid (north-east corner of Chatcombe Wood, Glos.) (7–8 prs.); plant S. 3 from Mercombe Wood (6–7 prs.); plant T. 7*b* from a woody slope above Withington Road (7 prs.). Second row: plant 170 from Birdlip, Glos. (5–6 prs.); plant 50 from Wiltshire Downs (6–7 prs.); plant C from Withington Road (5 prs.); plant M. 7 from Sapperton (7–9 prs.). In all leaflets the basiscopic margin is to the left. (×0·55.)

Fig. 8. Leaflets of octoploids from nature and culture. First row, plants grown at Kew: plant 111 from Uttoxeter, Staffs. (6 prs.); plant K. 5 from Chescombe Wood, Glos. (6 prs.); plant 18 from swampy ground in Hilcot Wood (5 prs.); plant 102 from Burlton Donhead St Mary, south Wilts. (4 prs.) plant 110 from Wargrave, Berks. (10 prs.); plant T. 16 from the bank of Thames-Severn Cana (6 prs.). Second row, plants from natural habitats: plant T. 8 from the bank of river Churn by Clifferdine, Glos. (4 prs.); plant T. 9 from a roadside bank between Marsden and Colesbourne Glos. (7 prs.); plant 144 from Avon Valley (4 prs.); plant T. 12 from the bank of river Churn by Perrotts Brook, Glos. (5 prs.); plant T. 16 from the bank of Thames-Severn Canal, Glos. (6 prs.). Third row, a series of conspicuously toothed leaflets of plants grown at Kew: plant 161, L. 3, from Somerset Levels (sedgemoor) (9 prs.); plant L. 8 from river Churn near Colesbourne (6 prs.); plant 162 from a sedgemoor in Somerset Levels (6 prs.); plant 25 from wet rocks above river Towy, by Ystrad-ffin, Carmarthen, Wales (6 prs.); plant T. 8 from river Churn by Clifferdine (4 prs.); plant T. 12 from river Churn by Perrotts Brook (6–7 prs.). In all leaflets the basiscopic margin is to the right. (× 0·50.)

Fig. 9. Relatively short and broad ovate leaflets of octoploids showing a very slight or irregular toothing of the basiscopic margin (on the right) and with the acroscopic margin (on the left) usually subentire. This group links up with some of the octoploids (Fig. 8, upper row), and some of the tetraploids (Figs. 4 and 7). All plants grown at Kew. From left to right: plant 84 from Iffley Lock, Oxon (6 prs.); plant N. 8 from Tavistock, south Devon (5 prs.); plant 48 from a swamp by Kirtlington, Oxon (6–7 prs.); plant T. 13 from roadside in a wood at Perrotts Brook (5 prs.); plant 40 from bank of watercourse at Kirtlington, Oxon (9 prs.). (× 0·55.)

Fig. 10. Leaflets of five giant octoploids from Sapperton, grown at Kew. From left to right: three sister plants, 8/3, 8/1, 8/2, grown from seeds of the giant plant 8 (open pollination); note the striking difference in shape and toothing (cp. Table 11); giant plant 6; giant plant M. 8. The basiscopic margin is on the right. (× 0·50.)

Some observations on the apical meristems of leafy and flowering shoots. By W. R. Philipson, B.A., Ph.D., F.L.S., Department of Botany, British Museum (Natural History)

(With Plate 9 and 1 Text-figure)

[Read 24 October 1946]

I. Zonation of the vegetative apex

The modern conception of the angiospermous stem apex as consisting of a central corpus enveloped in a tunica is now employed by most writers when describing apical meristems. Since the introduction of these terms by Schmidt (1924), their value has been demonstrated conclusively by much published work on periclinal chimeras (see, for example, Satina, Blakeslee & Avery, 1940, and Satina & Blakeslee, 1941, 1943).

In the opinion of the writer, however, the undoubted value of the 'tunica-corpus' concept has distracted attention from a zonation in the apical meristem of angiosperms which, when recognized, relates the angiospermous apex more closely with that found in gymnosperms. Pl. **9**, fig. 1, represents the apex of a lateral bud of *Succisa pratensis* Moench. which was fixed soon after growth had been resumed in spring. If the disposition of the meristematic cells is examined it is possible to recognize a two-layered tunica (periclinal divisions occur in the leaf-primordia) which overlies a massive corpus, but it is also evident that the corpus is not a uniform mass of meristematic cells. Within the corpus zones can be recognized by differences in the size of their cells and their avidity for stain. The centre of the corpus consists of large lightly staining cells with large nuclei; surrounding this central zone is a peripheral zone of smaller darker cells. Below the central zone, where the pith will develop, is a rib-meristem (see Text-fig. 1 *a*).

Very similar, but usually more striking, zonations have been described in gymnosperms. Koch (1891) described the occurrence of large central cells surrounded by smaller cells in the apices of conifers, but little attention was paid to this work until Korody's (1937) more modern investigations on *Abies*, *Picea* and *Pinus* confirmed the earlier account. Since that time American workers have described the apical meristems of many gymnosperms:

Cycadales: Forster, 1939, 1940 (*Cycas*); 1941 (*Dioon*); 1943 (*Microcycas*): Johnson, 1939 (*Zamia*); 1944 (*Encephalartos*, *Bowenia* and *Macrozamia*); 1945 (review of previous papers).

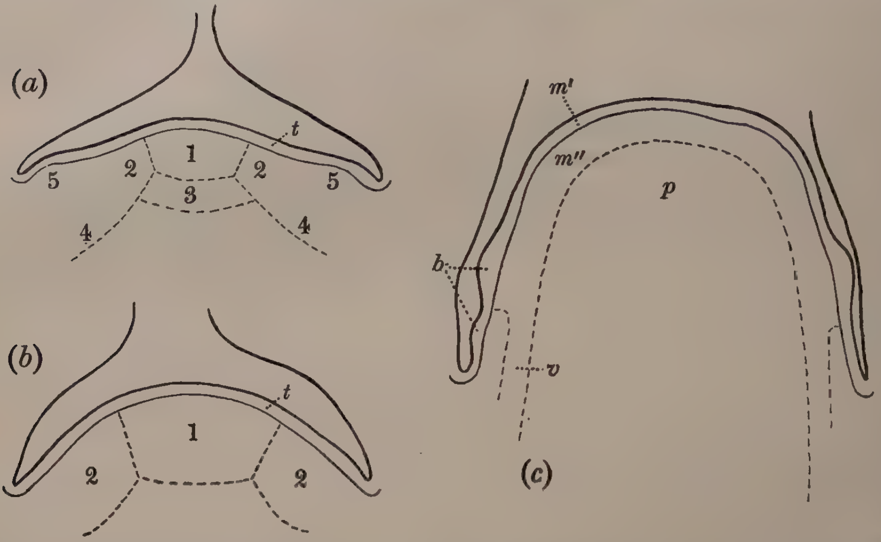
Ginkgoales: Forster, 1938; Gunckel & Wetmore, 1946.

Coniferales: Cross, 1939 (*Taxodium*); 1941 (*Cryptomeria*); 1942 (*Cunninghamia*); 1943 (*Sequoia*); 1943 *a* (*Athrotaxis* and *Taiwania*); Crafts, 1943 (*Sequoia*); Kemp, 1943 (*Torreya*); Hsü, 1944 (*Keteleeria*); Sterling, 1945 (*Sequoia*).

Gnetales: Gifford, 1943 (*Ephedra*).

As might be expected considerable differences of detail are found among these gymnosperm apices (for example, a definite dermatogen is present in *Ephedra*), but all agree in possessing a zonation essentially similar to that now described for *Succisa*. A similar zonation can be seen in the section of a lateral bud of *Sambucus nigra* L. represented in Pl. 9, fig. 2, which was cut tangentially with respect to the main axis. That the peripheral zone surrounds the apex on all sides is shown by Pl. **9**, fig. 3, which was taken from a similar bud of *Sambucus* but radially with respect to the main axis. Both buds were fixed in early summer and their apices were producing foliage-leaf primordia, for *Sambucus* does not produce flower-primordia until its shoots begin to elongate in spring. A zonation of this kind has also been observed in the corpus of the vegetative shoots of *Angelica*, *Valeriana*, *Dipsacus*, *Bellis*, *Dahlia* and *Lobelia*.

Several authors have recorded that the angiospermous apical meristem is not a uniform mass of equal cells, but have seldom regarded the zonation as significant. For example, it has been remarked frequently that the central cells of the tunica or corpus are comparatively large, and they may then be regarded as initial cells or groups of cells. Cros (1936) records such cells in the corpus of *Morus* and (1937) in the tunica of *Viburnum* Cross & Johnson (1941) remark on the occasional presence of a large cell in the tunica o *Vinca*. Langdon (1931) figures a central zone in the seedling apex of *Carya*, and Reev (1942) refers to a central zone in the corpus of *Garrya*. Esau (1942) records that in *Linum* the flanks of the apex are more densely meristematic than the extreme apex. Boke ha investigated the stem apex in a number of angiosperms. In his first paper (1940) h describes a zone of central mother cells in *Acacia*, but remarked that the distinguishin features of this zone were 'much more subtle than those which demarcate the shoot ape



Text-fig. 1. Diagrammatic longitudinal sections through the apices of lateral shoots of *Succisa pratensi* Moench. at three stages of development. (*a*) In spring, during the formation of foliage-leaves: 1, central zone of *large* cells; 2, peripheral zone; 3, rib-meristem; 4, provascular meristem; 5, foliage-leaf primordia; *t*, tunica. (*b*) Early stage of enlargement to form inflorescence rudiment: 1, central zone of *small* cells; 2, peripheral zone; *t*, tunica. *Note*: with cessation of growth in length the rib-meristem has disappeared. This section does not pass through provascular strands or earlier leaf-primordia. (*c*) Later stage of development of inflorescence: *b*, bract primordia, the upper cut medianly; *m'*, tunica; *m''*, corpus, corresponding to the central and peripheral zones of earlie sections; *m'* and *m''* together form the 'meristematic mantle'; *p*, 'parenchymatous core'. For a photograph of section (*a*) see Pl. 9, fig. 1, and for photographs of sections (*b*) and (*c*) see Philipson (1947, Pl. I, figs. 1, 2).

of *Ginkgo*'. In his later papers (1941, 1944) he describes zonation in the apices of cacti, but probably regards this structure as specialized rather than typical of angiosperms. Ball (1941) investigated the apices of a number of palms: *Washingtonia* and *Trachycarpus* are described as having apices with a zonation similar to that now described for *Succisa*, a condition which was recognized as general in dicotyledons. *Phoenix* has a larger and probably more specialized apex, though the division of the corpus into a central block meristem which gives rise to a peripheral zone and a rib-meristem is recognizable.

In one of his earliest papers on the structure of the apical meristem Forster (1935) describes the presence of a zone of initial cells in the corpus of *Carya*, and recognizes two regions in the remaining corpus cells, namely, a peripheral region and a central region of files of cells. Nevertheless, in the first of his reviews on the shoot apex Forster (1939) confines his treatment of the angiospermous apex to an account of the tunica and corpus, although the preceding account of the gymnospermous apex refers to zonations very similar to that of *Carya*. In his second review (1941) he recognizes that the tunica-corpus theory has perhaps distracted attention from other features, but he states that the zonal structure described by Boke for cacti does not correspond with that found in typical angiosperms but resembles rather that of *Ginkgo* or *Dioon*.

Engard (1944) divides the apices of seed plants into three groups on the basis of the organization of their meristematic cells. He puts all angiosperms into his first group which 'exhibit a tunica of one or more layers, and a central corpus of homogeneous cells'. Nevertheless, he describes and figures apices of *Rubus* in which the corpus is not strictly homogeneous as it includes a group of initial cells. He attributed the presence or absence of a rib-meristem below the corpus to the rate of elongation of the axis.

Two authors have recognized the general occurrence of zonation in the apical meristems of angiosperms. Majumdar (1942) defines the flank meristem as follows: 'More detailed analysis of the eumeristem tends to show that it usually consists of a group of central initial cells over the actual summit of the apical cone and the lateral flank meristem down the sides of the cone. In the central region the meristem cells have characteristics suggesting that they are less actively meristematic than those of the flank meristem, and whilst the former constitute the self-perpetuating meristem of the apex, the flank meristem contributes to leaf formation.' Mitra (1945) follows Majumdar in describing similar zones in the vegetative apex of *Polygonum orientale* L. Apart from *Heracleum*, with which his paper was concerned, Majumdar did not cite evidence in support of his general statement, nor did he relate the zonation with that of gymnosperms. Both these omissions are made good in his Presidential Address before the Indian Science Congress at Nagpur (Majumdar, 1945). The Chinese botanist Hsü (1944) also cites a number of authors who have described apices similar to that which he figures for *Sinocalamus* and has seen in a number of other plants, both gymnospermous and angiospermous. I arrived independently at the same conclusions as Majumdar and Hsü, and when the zonation of *Bellis* was described as typical of that found in many angiosperms (Philipson, 1946), their papers had not been available to me owing to war conditions.

In concluding this section it should be emphasized that the number of angiosperm apices which have been examined with modern technique is still very small. However, the number of species belonging to diverse groups of flowering plants which show zonation in the corpus is regarded as significant. In many dicotyledons the apex is so small as almost to be non-existent, but in my experience the central cells always show differentiation from those on the periphery. In comparing this zonation with that found in gymnosperms, no comparison of detail is intended (in any event, wide variation of detail is found within the gymnosperms themselves), but rather a broad comparison which recognizes the presence of a central zone surrounded by a 'more meristematic' peripheral zone. On this basis there would be a general resemblance between the meristematic zones in the apices of gymnosperms and angiosperms, a resemblance that may be heightened in the exaggerated apex found in cacti. It is the recognition of such basic resemblances which will form a sound foundation for the systematic investigation of differences which may be discovered between the apices of different plant groups. It may well be, however, that differences in apical organization will be found to be more characteristic of habit-types than of taxonomic groups.

II. ZONAL CHANGES AND REPRODUCTION

Grégoire (1938) described the meristems present in the rudimentary flowers of a considerable number of plants. As is well known, he recognized the presence of a meristematic mantle which covered the reproductive apex uniformly, and which enclosed a parenchymatous core of more mature cells. Pl. 9, figs. 4 and 5, illustrate these two regions in the young inflorescences of *Bellis perennis* L. and *Angelica sylvestris* L. respectively. The darkly staining zone of cells surrounding the receptacle of *Bellis* and each partial umbel of

Angelica constitutes the mantle; the lighter, more mature cells within form the parenchymatous core. Grégoire compared this type of apex with that of the vegetative shoot, and considered that the two were absolutely distinct. While the value of Grégoire's work from the purely descriptive point of view is indisputable, his hard and fast division of the plant into vegetative and reproductive regions has been criticized. This criticism has been, first, on the general ground that the plant should be regarded as an organism whose development towards reproduction is a function of all its parts, a point of view receiving much support from plant physiology. Secondly, the morphological evidence on which Grégoire based his conclusion has not always been confirmed by later research. For example, Grégoire described the acropetal development of provascular meristems in floral apices and contrasted this condition with the mode of development of leaf-traces, which at that time were thought to originate at the base of the leaf and differentiate both upwards and downwards from that point. Subsequent work has shown that the provascular meristems of vegetative shoots of both gymnosperms and angiosperms develop acropetally (see, for example, Priestley & Scott, 1936; Majumdar, 1940; Boke, 1940; Reeve, 1942; Esau, 1943; Crafts, 1943*a*; and Gunckel & Wetmore, 1946*a*; but compare Hsü, 1944, who records the initiation of provascular tissue at the base of the leaf in a bamboo). The distinction between the mode of development of the vascular tissue in the flowering and the leafy shoot has, therefore, broken down.

It is not intended to examine all the criteria which Grégoire considered to characterize his two morphological regions of the plant, but rather to re-examine his primary criterion—the distribution of the apical meristems. Grégoire accepted the current view that the apical meristem of the vegetative apex may be divided into tunica and corpus, but thought this terminology inappropriate to the reproductive apex, which lacks a central meristematic mass, and, as we have seen, used the terms 'meristematic mantle' and 'parenchymatous core'. Engard (1944) considered that the meristematic mantle was equivalent to the tunica of the vegetative apex, and proposed to replace Grégoire's terms with 'reproductive tunica' and 'reproductive corpus' respectively. Several recent authors, however, have applied the term tunica to the reproductive apex in a different, and it would appear more correct, sense (Brooks, 1940; McCoy, 1940; Satina & Blakeslee, 1941; Reeve, 1943; Majumdar, 1945; Philipson, 1946; Miller & Wetmore, 1946). These authors regard the tunica as those superficial layers whose cells divide predominantly in an anticlinal direction. The tunica layer may vary in depth, but it can be recognized in apices at all stages of development. There is no justification, therefore, for extending the term to include all the meristematic tissues of the reproductive apex, for the mantle comprises, in addition to the regular superficial layers, an inner zone of less regularly arranged meristematic cells. In Pl. 9, figs. 4 and 5, the two outer layers of cells are regularly arranged and constitute the tunica; these two layers, together with the other darkly staining cells immediately within them, constitute the mantle. In what follows an attempt will be made to show that these inner cells of the mantle are derived from the corpus.

In approaching the problem of the relationship between the vegetative and the reproductive apex from a consideration of the meristematic zones present in each, it is necessary to trace the developmental history of these zones during the transformation of the apex from the vegetative to the reproductive state. Usually this change will not be direct to the rudiment of a flower but to that of an inflorescence. The validity of the comparison will not be affected, however, because although Grégoire dealt mainly with floral apices, he extended his concept to the apices of inflorescence rudiments, which he showed to possess a meristematic mantle and parenchymatous core identical with those of the flower.

The transformation of an apex from the vegetative to the reproductive type of zonation is so rapid that it has proved exceedingly difficult to trace. In conformity with his view that the meristematic zones of vegetative and reproductive apices are not comparable, Grégoire did not consider the inflorescence rudiment to be a transformed vegetative apex but to be a new outgrowth arising from its flank. Several subsequent investigators, however, have shown that the inflorescence arises by the modification of the apex of an axis. It remains to trace the details of this transformation.

In 1946 I described the replacement of the central zone by the peripheral zone to form the mantle in the young capitula of *Bellis perennis* L., but *Succisa pratensis* Moench. has proved a more suitable subject. In this scabious the main axis remains sterile, the flower-heads being borne on lateral shoots. The buds of these shoots form in autumn and remain dormant during the winter. When they resume growth in spring their apical meristems show the typical vegetative zonation, with a tunica and a corpus comprising a central zone of large cells, a dark-staining peripheral zone, and a rib-meristem (see Pl. **9**, fig. 1). After producing one or two pairs of leaves these shoots are dominated by their primary function of flower production, and though still forming leaf-like bracts their central zone of large cells no longer maintains its identity, being replaced by smaller cells similar to those of the peripheral zone. Nevertheless, the peripheral zone continues for some time to be distinguishable. A photograph of this type of apex has been included in an account of the development of the inflorescence of *Succisa* together with a photograph of a subsequent stage when all trace of the central zone has been lost, the mantle then being lined throughout by a uniform zone of irregularly arranged cells (Philipson, 1947, Pl. 1, figs. 1, 2). The three stages of this transformation are represented diagrammatically in Text-fig. 1.

The transformation from the zonation of the vegetative apex to that of the reproductive apex that has just been described shows that the terms proposed by Engard for describing the regions found in the reproductive apex are invalid. The mantle is not equivalent to the tunica alone, but to the tunica and the corpus, which latter has become a thin uniform lining rather than a bulky differentiated mass. Similarly, the parenchymatous core is not equivalent to the corpus, or at most to no more than the rib-meristem, for it represents the maturing pith cells of the inflorescence axis.

The occurrence in vegetative apices of a zonation of the type described in the first part of this paper may possibly be regarded as additional evidence in favour of Grégoire's concept of the leafy shoot and the flower as irreducible morphological types. This zonation is different from that of the reproductive apex, but in view of the simple changes which bring about the transformation it seems inadvisable to place much weight on this difference. It appears preferable to regard the apex as essentially similar in both states: these differ merely in the degree of development of the different meristematic zones, no doubt due to the different directions in which growth is taking place in the elongating shoot and the developing flower or inflorescence.

Summary

1. The arrangement of cells at the apex of vegetative shoots of angiospermous plants is examined, and it is concluded that the corpus is not a homogeneous meristem but exhibits the following zones: (i) a central zone of large, lightly staining cells; (ii) a peripheral zone of smaller, darkly staining cells; and (iii) a rib-meristem.

2. The essential similarity between this zonation and that found in gymnosperms is discussed.

3. The relationship between this zonation and that first described by Grégoire for the reproductive apex is investigated by tracing the transformation from one to the other in *Succisa*. It is concluded: (i) that the outer layers of the mantle correspond with the tunica of the vegetative apex, and (ii) that the inner layers of the mantle represent the corpus, which has lost its former division into zones, all its cells resembling those of the peripheral zone.

4. The bearing of this transformation on the morphology of the leafy shoot and the flower is discussed, and it is considered that the organization of the apical meristems should not be regarded as essentially different in the vegetative and the reproductive state.

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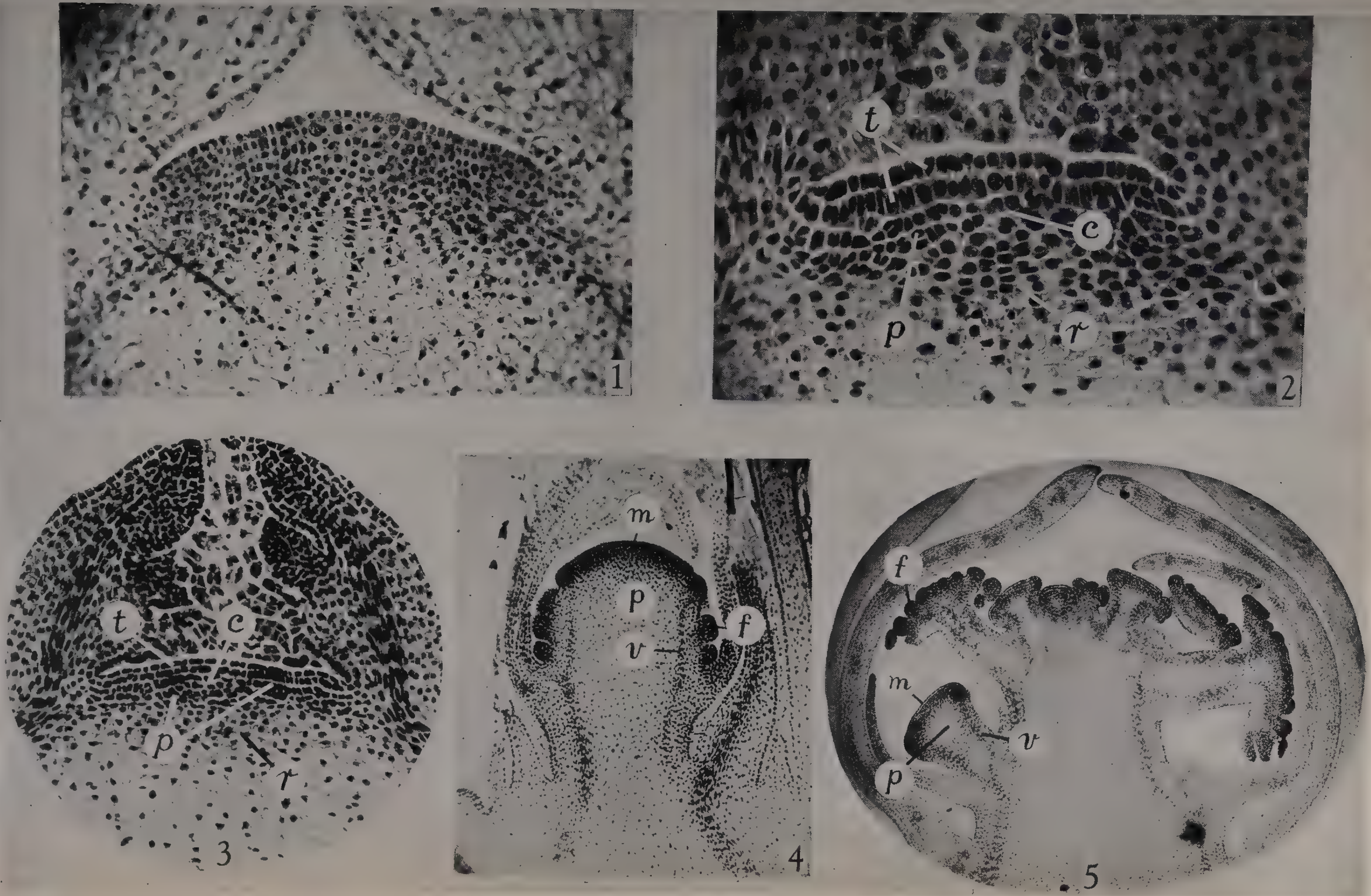

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EXPLANATION OF PLATE 9

Fig. 1. Longitudinal section through vegetative apex of *Succisa pratensis* Moench. For explanation see Text-fig. 1.

Fig. 2. Longitudinal section through lateral bud of *Sambucus nigra* L., cut tangentially with respect to the main axis. *c*, central zone; *p*, peripheral zone; *r*, rib-meristem; *t*, tunica.

Fig. 3. Longitudinal section through similar bud of *Sambucus*, cut radially with respect to the main axis. Lettering as in previous figure.

Fig. 4. Longitudinal section through capitulum of *Bellis perennis* L. *f*, floret-primordium; *m*, 'meristematic mantle'; *p*, 'parenchymatous core'; *v*, provascular meristem.

Fig. 5. Longitudinal section through compound umbel of *Angelica sylvestris* L. Lettering as in previous figure.

The nomenclature and synonymy of Tofieldia calyculata and T. pusilla. By William T. Stearn, Lindley Library, Royal Horticultural Society, London, S.W. 1

(With 3 Text-figures)

[Read 20 February 1947]

The genus *Tofieldia* Hudson, as defined by K. Krause in Engler & Prantl, *Nat. Pflanzenfam.* 2nd ed. **15***a*, 254 (1930), comprises about eighteen species. The Scottish asphodel, commonly known as *T. palustris* Hudson, is the only one occurring in Britain and Scandinavia exclusive of Gotland. For this the names *T. borealis* (Wahlenb.) Wahlenb. and *T. minima* (Hill) Druce have also been widely used. The purpose of the following article is to present the historic, taxonomic and geographical background to the nomenclature and synonymy of the Scottish asphodel and thus to demonstrate that its correct name is *T. pusilla* (Michx.) Pers.

The nomenclature of this plant being entangled with that of *T. calyculata* (Linn.) Wahlenb., the two species must be considered together. Although Linnaeus made no specific distinction between them, they differ markedly in many characters, including those of size, leaf and inflorescence, as well as in ecology and distribution.

The Scottish asphodel (*T. palustris* auct.) is a tiny plant, possibly the smallest member of the Liliaceae. Its iris-like leaves are usually three-veined (but sometimes four-veined) and under 5 cm. long; its inflorescence is a clustered head of up to ten white or greenish white flowers on a stem about 10 cm. (rarely up to 22 cm., sometimes down to 1·5 cm.) high, with a small three-lobed bract subtending each pedicel but with no bracteole immediately beneath each flower. *T. calyculata*, on the other hand, is more vigorous, with 3–11-veined gradually acuminate leaves up to 23 cm. long; its yellowish flowers are more numerous and more loosely disposed, forming usually a cylindrical inflorescence (sometimes 7 cm. long) on a stem 7–45 cm. high; a small undivided bract subtends each pedicel and there is a small, slightly three-lobed involucral bracteole or 'calyculus' (called a 'perianth' by Linnaeus) immediately beneath each flower. From this last feature (more evident in fruiting than in flowering material; cf. Fig. 2*a*) the plant takes its name.

The Scottish asphodel is a circumpolar and alpine species (cf. Figs. 1, 2). It ranges, with many breaks, from Greenland over northern North America, northern Siberia, northern European Russia, Scandinavia, Spitsbergen and northern Britain to Iceland: it occurs also in the Alps, between 1800 and 2670 m. (fide Hegi). Comparison of Canadian and Greenland specimens with British, Scandinavian and Iceland specimens in the Cambridge, Kew and Oxford herbaria confirms the general opinion that the American and European plants belong to the same species. *T. calyculata* ranges from the Pyrenees eastward to south-western European Russia and from the Alps and Balkan Peninsula northward to Estonia and the Baltic islands of Gotland, Oesel (Saare Maa) and Moon (Muhu); in the Alps it occurs mostly in subalpine regions and on Gotland I found it almost at sea-level. Thus *T. calyculata* is essentially a central European subalpine or lowland species, whereas the Scottish asphodel is an Arctic or high-alpine one. Only in the Alps, where they mostly grow at different heights, do their ranges overlap. The Scottish asphodel seems rarely if ever to survive for long in gardens. *T. calyculata*, on the other hand, has grown for over 15 years in a moist part of the rock garden at Kew without special care, and Baxter in 1837 figured a plant which had 'for many years, probably ever since the time of Dillenius [died 1747], been cultivated in the Oxford Garden'.

The credit for first distinguishing the two species satisfactorily rests with the Swedish botanist Göran Wahlenberg (1780–1851), but the literature relating to them begins with the discovery of *T. calyculata* in Austria by Charles de l'Ecluse [Carolus Clusius] (1526–1609) and of the Scottish asphodel in Scotland by John Ray (1627–1705). To interpret their synonymy one must go back to these pre-Linnaean authors.

Clusius came across the species now called *T. calyculata* when botanizing in the Schneealpen and near Neuberg in Lower Austria. He described and figured it in 1583 as *Pseudoasphodelus pumilio foliis Iridis* (Fig. 3A), a name transformed into *P. alpinus* by Gaspard Bauhin in 1623 and into *Phalangium Alpinum, palustre, Iridis folio* by Tournefort in 1700. None of these pre-Linnaean authors seems to have noticed the inconspicuous 'calyculus'; but their figures, localities and measurements establish their plant as identical with the modern *Tofieldia calyculata*. By 1745 this was known to grow in northern Italy,

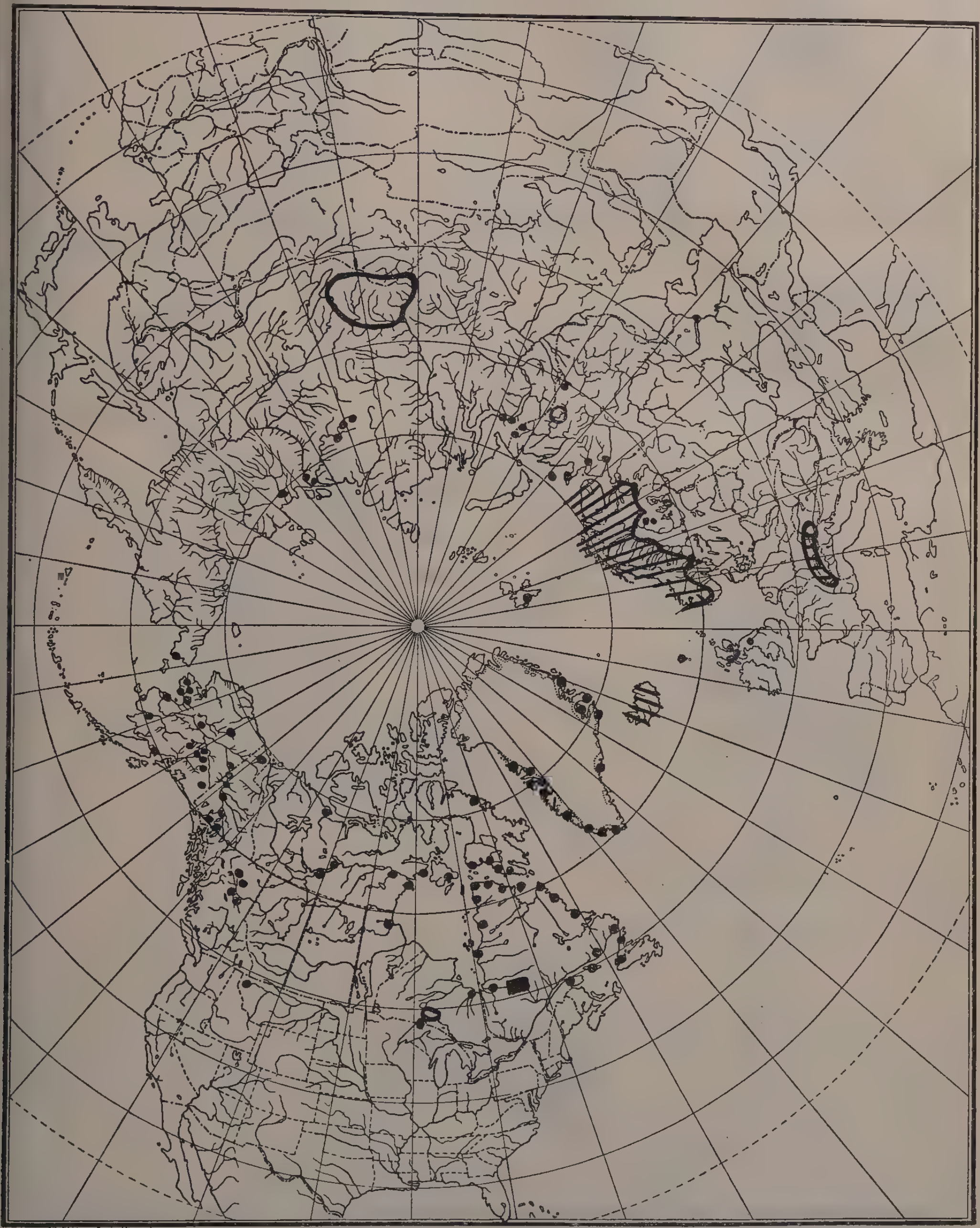

Fig. 1. Distribution of *Tofieldia pusilla* (■ type region; **IIII** numerous localities, ○ unverified).

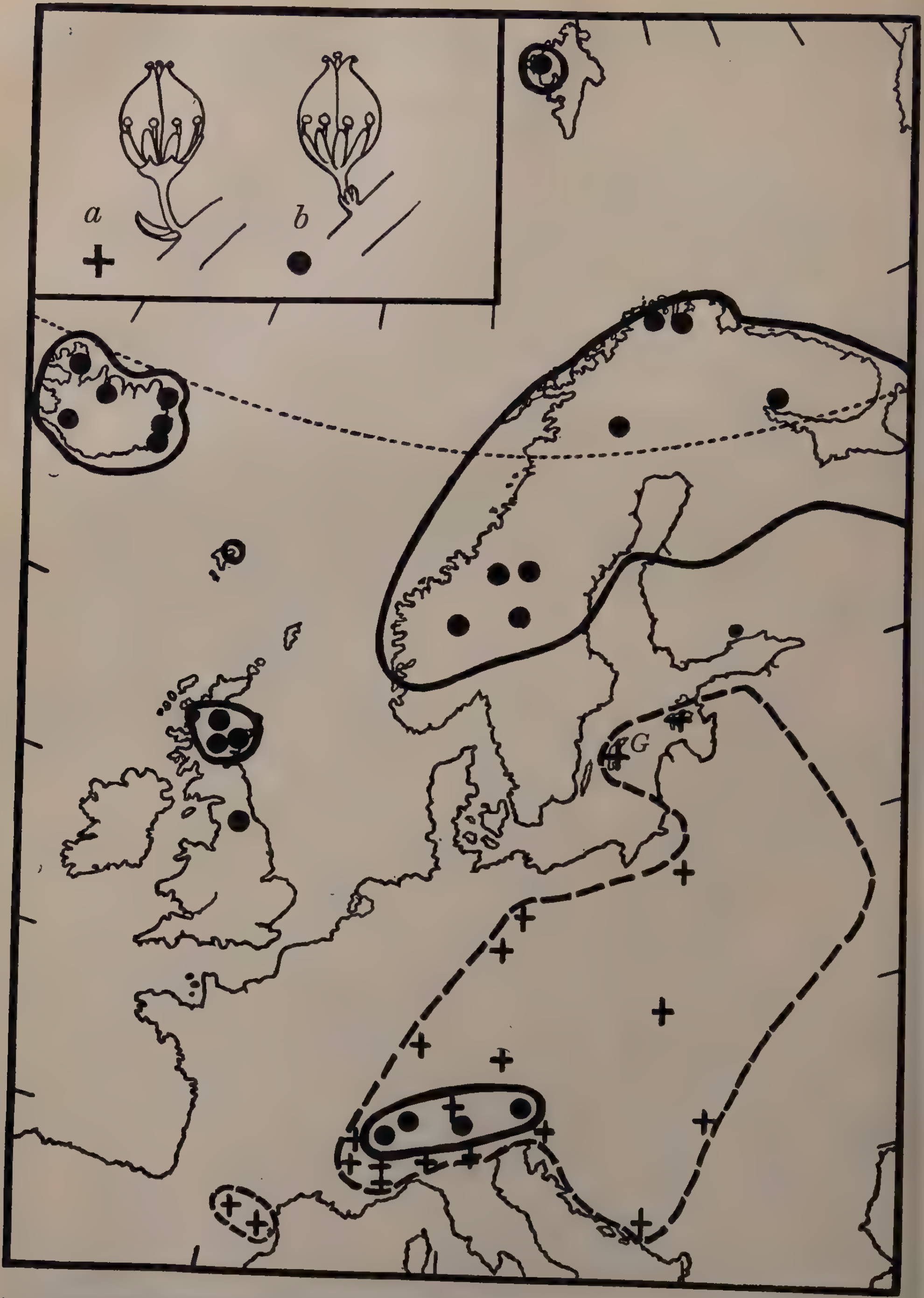

Fig. 2. European distribution of *Tofieldia pusilla* (—— general boundary; ● localities from which specimens have been examined in British herbaria). *T. calyculata* (- - - general boundary; + localities from which specimens have been examined in British herbaria; *G*=Gotland). Inset above: fruiting material of (*a*) *T. calyculata*, (*b*) *T. pusilla*, diagrammatically portrayed.

Switzerland, Savoy and Gotland as well as Lower Austria. In the meantime (1677) Ray had recorded our Scottish asphodel from Scotland[1] under the name of *Asphodelus palustris Scoticus minimus* which Tournefort transformed into *Phalangium Scoticum, palustre, minimum, Iridis folio*. Linnaeus found the same species in Lapland in 1732 and described and figured it in his *Flora Lapponica* (1737) as *Anthericum scapo nudo capitato, filamentis glabris* (Fig. 3 B). During his stay in Holland from 1735 to 1738 another species came to his notice; it had been sent to his patron and devoted helper, the Leiden senator Jan

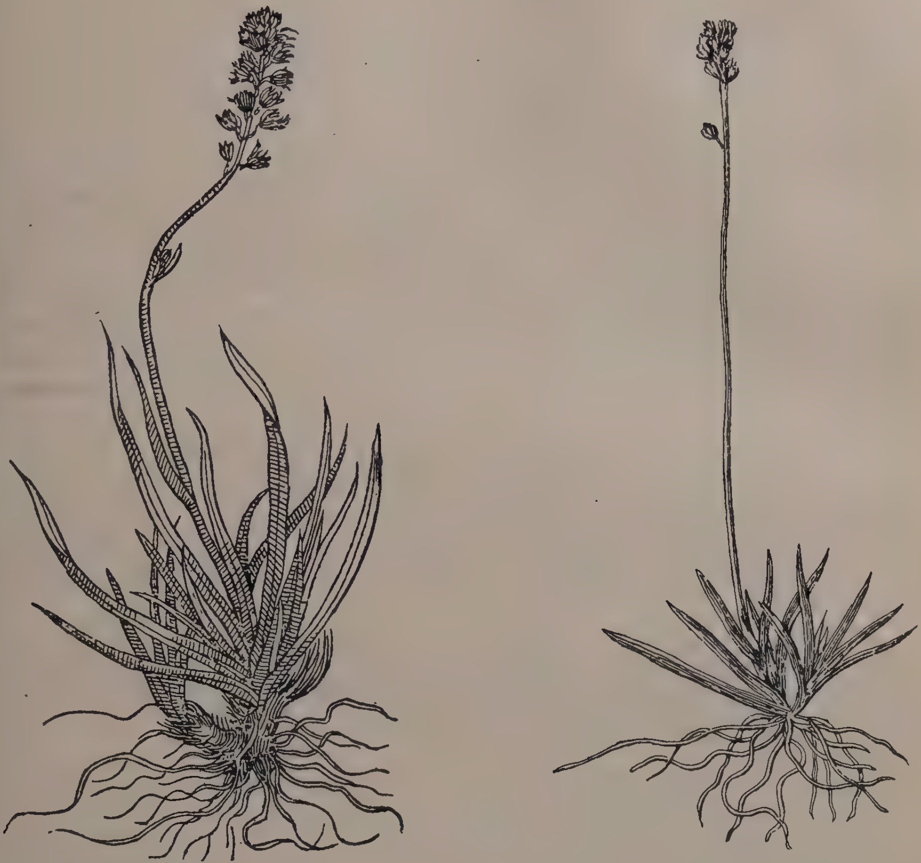

Fig. 3 A. **Fig. 3 B.**

Fig. 3. A. *Tofieldia calyculata* (L.) Wahlenb., *Pseudoasphodelus pumilio* Clusius [from Clusius, *Rar. Stirp. Pannon.* 261 (1583)]. B. *Tofieldia pusilla* (Michx.) Pers., *Anthericum scapo nudo capitato* Linn. [from Linnaeus, *Fl. Lappon.* t. 10 (1737)].

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[1] Ray knew the continental *Tofieldia calyculata* which is represented in his herbarium at the British Museum (Natural History) by a specimen named *Pseudoasphodelus palustris* (fide J. E. Dandy in litt.), so there seems no doubt that the plant he described as *Pseudoasphodelus* (or *Asphodelus*) *palustris Scoticus minimus* is the Scottish asphodel, even though this has not been found again in the locality from which he recorded it: 'about two miles North of Barwick' (Ray, *Cat. Plant. Angl.* 2nd ed. 30, 1677). In an entry for 23 July 1671 in his posthumous Itineraries (see Lankester, *Memorials of John Ray*, p. 151, footnote, 1846) he is even more definite: 'About two miles from Berwick, by the side of a rivulet, in a boggy ground, not far from the road leading to Edinburgh, we found a sort of *Pseudoasphodelus* which I had never before seen, much less than that common in England [i.e. *Narthecium ossifragum*], having, as I guess, white flowers in a spike to which succeed rounded seed vessels. The stalk of the spike is naked or not having above one leaf, the spike itself short, the root fibrous, as that of the common.'

Fredrik Gronovius, from Virginia and was remarkable in possessing a minute three-lobed 'perianthium' or 'calyculus' beneath the flower. This American species, now known as *Tofieldia racemosa* (Walter) B.S.P., *T. pubens* (Michaux) Willd. or *Triantha racemosa* (Walter) Small, he described in the *Hortus Cliffortianus* (1737) as *Anthericum filamentis laevibus, perianthio trifido.* A few years later (June–July 1741) Linnaeus visited Gotland and found the robust species now called *Tofieldia calyculata*; but he regarded it as merely a larger form of the plant he had previously found in Lapland. Sir James E. Smith's statement, that Linnaeus 'strongly suspected the two plants to be different, but never, to the day of his death, saw more than one of them', is disproved by Linnaeus's own account of his Gotland journey (*Öländska och Gothländska Resa*, 1745). This Gotland plant he enumerated in 1741 under the name *Anthericum foliis ensiformibus, filamentis glabris*, with his earlier (1737) *A. scapo nudo* from Lapland as a synonym. By 1745 he had noticed that the Gotland plant possessed a three-cleft calyx or 'perianthium' like that to which Gronovius had previously called his attention in the American species. He accordingly re-named the Gotland plant *A. foliis ensiformibus, perianthiis trilobis, filamentis glabris*, and apparently assumed that the Lapland plant likewise possessed a 'calyculus'. Linnaeus described his Gotland journey in Swedish, a language with which Smith was not familiar; otherwise he would not have overlooked Linnaeus's note (here translated) on the *Anthericum* growing near Hau: 'A herb, which I had previously found only in Lapland and described in *Flor. Lapp.* n. 137 t. 10 f. 3, occurred in great abundance lower down in the same meadow close to the bog; the Gotland plant was bigger as regards the stalk and flowers and had a more pointed pistil, which was three-styled (trigyna) like the Lapland one. The same herb was remarkable in possessing a three-cleft calyx (et treklufdt Blomfoder), whereas none of its kind or group has any calyx; this [feature] the learned botanist Fr. Gronovius had already pointed out to me on the plant which he had received from Virginia in America.'

By 1753 Linnaeus had come to regard all three—the Lapland, the Virginian and the Gotland plants—together with a Siberian one, as conspecific and needing but one name between them. The synonymy given under *Anthericum calyculatum* in his *Species Plantarum* (1753), **1**, 311, is as follows [with explanations added in square brackets], and covers them all:

'Anthericum foliis ensiformibus, perianthiis trilobis, filamentis glabris. *Fl. suec.* 269 [i.e. Linnaeus, *Fl. Suecica*, 95, no. 269 (1745) which refers back to *Kongl. Svenska Vetensk. Akad. Handl.* **2**, 191 (1741), the first mention of the Gotland species to which the name *Tofieldia calyculata* is now restricted]. *It. gotl.* 194. 221 [i.e. Linnaeus, *Öländska och Gothländska Resa*, 194, 221 (1745), where this Gotland plant is discussed at greater length and its three-lobed bracteole or 'calyculus' first noted].

'Anthericum filamentis laevibus, perianthio trifido. *Hort. cliff.* 140 [i.e. Linnaeus, *Hortus Cliffortianus*, 140 (1737), describing the Virginian species now called *Tofieldia* (or *Triantha*) *racemosa*]. *Gron. virg.* 39 [i.e. Gronovius, *Fl. Virginica*, 39 (1739).]

'Anthericum scapo nudo capitato, filamentis glabris. *Fl. lapp.* 139. t. 10, f. 3 [i.e. Linnaeus, *Fl. Lapponica*, 100 no. 137, t. 10 fig. 3 (1737), giving an account of the Lapland species now called *Tofieldia pusilla*].

'Phalangium alpinum palustre, iridis folio. *T. Segu. ver.* 2, p. 61, t. 14 [i.e. Seguier, *Plantae Veronenses*, **2**, 61, t. 14 (1745), figuring and describing from northern Italy the species now called *Tofieldia calyculata*].

'Pseudo Asphodelus alpinus. *Bauh. pin.* 29 [i.e. C. Bauhin, *Pinax*, 29 (1623), which refers back to the description and figure of *Pseudo-asphodelus II*, i.e. the modern *Tofieldia calyculata*, in Clusius, *Rariorum Plant. Hist.* 198 (1601), which repeats the description and figure in Clusius, *Rariorum aliquot Stirpium per Pannoniam*, 261 (1583)].

'*Habitat in alpibus* Helvetiae [i.e. *Tofieldia calyculata* sensu stricto], Lapponiae [i.e. *T. pusilla*, the Scottish asphodel], Sibiriae [i.e. *T. cernua* Smith; cf. Smith in *Trans. Linn. Soc.* **12**, 244 (1818)].'

Thus Linnaeus's account of his *Anthericum calyculatum*, as the above analysis shows, refers principally to the central European and Gotland species with a 'perianthium' or 'calyculus'. To this species authors have consistently restricted the name *Tofieldia calyculata* (Linn.) since the time of Wahlenberg. The plant in the Linnaean herbarium under the epithet *calyculatum* (Herb. no. 342, 14) belongs, however, to a Siberian species *T. cernua* Smith and bears a label in the handwriting of Johann Amman (1707–41): 'Anthericum filamentis levibus, perianthio integerrimo. No. 12.'

The Linnaean genus *Anthericum* as accepted in the *Species Plantarum* of 1753 did not long keep intact; indeed, Linnaeus himself was inclined to divide it into three genera (*Anthericum*, *Bulbine* and *Narthecium*, the last including *Tofieldia*), and to-day only three (*A. revolutum*, *A. ramosum* and *A. Liliago*) of the original ten species remain in *Anthericum*. *Bulbine*, *Narthecium* and *Tofieldia* possess the others.

In 1762, William Hudson restored Moehring's genus *Narthecium* for *Anthericum ossifragum* Linn. At the same time he recorded the Linnaean species *A. calyculatum* from Britain, using Linnaeus's diagnosis and citing as synonyms both *Pseudo-asphodelus alpinus* Bauhin and *Pseudo-asphodelus palustris Scoticus* Ray. In the second edition (1778) of his *Flora Anglica*, Hudson restricted the genus *Anthericum* to *A. serotinum* (i.e. *Lloydia serotina*) and established a new genus, *Tofieldia*,[1] for *Anthericum calyculatum*, basing his generic description on the British plant but making no distinction between this and the calyculus-bearing continental species; he adds references to the latter plant from Scopoli and Haller. Accepting the Linnaean concept of the species, Hudson ought (by modern standards) to have accepted the Linnaean specific epithet *calyculatum* too, but this he changed to *palustris*. Hence the name *Tofieldia palustris* as first published must be regarded as a new name for *Anthericum calyculatum* Linn. Having this as its type it becomes a synonym of *Tofieldia calyculata* and cannot legitimately be used for the British and Lapland plant later separated from *T. calyculata*. Therefore a specific name other than *palustris* must be found for the Scottish asphodel. Michaux provided this in 1803. As already noted, the species extends from Scandinavia and Britain over Iceland and Greenland to eastern Canada. Here in 1792 it was found by André Michaux near Lake Mistassini, Quebec (cf. ■ Fig. 1). Michaux (or more likely L. C. Richard, whose part in the preparation of Michaux's posthumous *Flora Boreali-Americana* is known to have been large) described it early in 1803[2] as a new species, *Narthecium pusillum*, with a diagnosis which satisfactorily distinguishes the plant from *T. calyculata*:

'PUSILLUM. N. laeve glabrumque: foliis brevissimis: scapo filiformi: spica pauciflora, conglobata: calyculo rachi adnato: capsula globosa. OBS. Affine *N. alpino* sive ANTHERICO *calyculato*; omnibus partibus minus: calyculo non immediate sub calyce, sed rachi innato et basim pedicelli cingente. HAB. ad lacus Mistassins' (Michaux, *Fl. Boreali-Amer.* **1**, 209).

Michaux's material is in Paris at the herbarium of the Muséum d'Histoire Naturelle. In 1939 Mr Charles E. Weatherby of the Gray Herbarium kindly compared Michaux's material for me with specimens of the Scottish asphodel from Perthshire (Corrie Buidheag, Ben Lawers, Ben Laoigh, *herb. Francis Druce*)[3] and found no difference between them. From his detailed report the following description of Michaux's three specimens is taken:

Leaves 2–4·5 cm. long, 1–2·25 mm. wide, three-veined (rarely with a poorly developed fourth vein) with minutely scabrous margins; *fruiting stems* 18 cm., 9·5 cm., 13 cm. high; *raceme* in fruit 6·5 mm., 10 mm., 14 mm. long; *bracts* either entirely gone or in poor condition but apparently lobed and certainly at the base of the pedicels, not just below the flower; *pedicels* 1·5–2 mm. long; *tepals* more or less withered, about 1·5 mm. long, 0·6 mm. broad, somewhat spatulate; *capsule* about 2·5 mm. long, exclusive of style; *style* 0·5 mm. or less. British and Scandinavian specimens match these details closely. In 1805 Persoon transferred *Narthecium pusillum* to *Tofieldia* as *T. pusilla*, and that is the name which must now be adopted for Michaux's species and the British, Scandinavian and Alpine plants conspecific with it.

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[1] Hudson does not give the derivation of the name *Tofieldia* but undoubtedly it commemorates his Yorkshire correspondent Thomas Tofield (1730–79) a country gentleman who was the first to find *Vicia bithynica* in Britain. The surname Tofield, like Tuffield and Tuffill, is a variant of the obsolescent Middle English 'to-fall' meaning a lean-to or penthouse (cf. Weekley, *Surnames*, p. 82; 1917).

[2] In *Rhodora*, **44**, 149 (1942), Miss Bernice G. Schubert has proved that Michaux's *Flora Boreali-Americana* was published before 19 March 1803.

[3] These specimens were destroyed by an air raid on London in May 1941 in which Mr Francis Druce lost his life.

In 1805, i.e. two years after the publication of *Narthecium pusillum*, Wahlenberg, investigating the flora of Gotland, noted the heterogeneous nature of Linnaeus's *Anthericum calyculatum* and took as the type of the species the plant which grows here and there on the island in low-lying boggy ground. He named it *Narthecium calyculatum*. The Lapland plant, '*Tofjeldia palustris* Anglorum', he described as a new species under the name of *Narthecium boreale*. In 1812 (*Fl. Lappon.* 90) he called the one *Tofieldia calyculata* and the other *T. borealis*. Both *Narthecium boreale* Wahlenb. and *Tofieldia borealis* (Wahlenb.) Wahlenb. were published independently of *Helonias borealis* Willd. (1799), which, like the earlier *Tofieldia palustris* Hudson, was a new name for *Anthericum calyculatum* Linn.; Willdenow's citations cover both *Tofieldia calyculata* sensu stricto and *T. pusilla*, but Willdenow's diagnostic phrase 'bracteis duplicatis' (i.e. having both bract and 'calyculus') applies only to the former.

Wahlenberg's conclusions as to the distinctness of the two species were accepted by Count Kaspar von Sternberg and David Hoppe in an illustrated memoir published in 1815 (*Denkschr. Bot. Ges. Regensburg*, **1**, 148–55), and the presence of the Scottish asphodel in the Alps was clearly established by them. But instead of accepting Wahlenberg's nomenclature they adopted the name *T. palustris* for *T. calyculata* sensu stricto and gave a new name, *T. alpina* Sternb. & Hoppe, to the Scottish asphodel (*T. pusilla*).

Unaware of the work of Wahlenberg, Sternberg and Hoppe, Sir James E. Smith published in 1818[1] a 'Botanical history of the genus *Tofieldia* (*Trans. Linn. Soc. Lond.* **12**, 235–47), wherein, with customary precision, he described six species of *Tofieldia* and unravelled their synonymy. He seems to have overlooked Linnaeus's visit to Gotland and supposed Linnaeus to have been personally acquainted only with the Lapland plant. Moreover, like other botanists of his day, Smith was bound by no rigid rules of nomenclature and evidently believed himself entitled to exercise 'that discretionary paramount authority, which belongs only to the leaders in Botany, of overruling a prior claim of nomenclature'! He took the Linnaean name *Anthericum calyculatum* as applying primarily to the Scottish asphodel for which he adopted the name *Tofieldia palustris*. To *T. calyculata* sensu stricto he gave a new name, *T. alpina* Smith. Smith's nomenclature is thus the reverse of Sternberg and Hoppe's. Later botanists have rejected the name *T. alpina*, but the majority have followed Smith in using the name *T. palustris* for the Scottish asphodel.

In 1914, G. Claridge Druce put forward the name *T. minima* (Hill) Druce, based on *Phalangium minimum* Hill, *British Herbal*, 473 (1756). This work of John Hill's is of pre-Linnaean character; phrase names occur in it side by side with binomials. Thus, while the Scottish asphodel, Hill's 'Dwarf Bastard-Asphodel', is called *Phalangium minimum*, the bog asphodel (*Narthecium ossifragum*) is called *Phalangium iridis folio majus*. Under the *International Rules of Botanical Nomenclature*, 3rd ed., art. 68 (1935), specific epithets are illegitimate and must be rejected if originally published in works wherein the Linnaean system of binary nomenclature is not consistently employed. Hence neither Hill's name nor Druce's has any validity; neither competes with *Tofieldia pusilla*, as the plant concerned must be called.

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[1] Smith's 'Botanical history of the genus *Tofieldia*' was read to the Linnean Society of London on 21 January 1817 but vol. 12, part 1 of the Society's *Transactions* did not appear until early 1818 (cf. Stearn in *J. Bot.* **71**, 26, footnote, 1941). In the meantime he published a summary in Rees, *Cyclopaedia*, **35** (part 70, May 1817, *fide* Jackson in *J. Bot.* **34**, 311, 1896) and the names *T. alpina* Smith, *T. stenopetala* Smith and *T. cernua* Smith accordingly have their first publication here.

The following is the synonymy of the two species:

1. TOFIELDIA CALYCULATA (Linn.) Wahlenberg.

Pseudo-asphodelus pumilio foliis Iridis Clusius, *Rar. Stirp. Pannon.* 261 cum icone (1583).

Pseudo-asphodelus II Clusius, *Rar. Plant. Hist.* 198 cum icone (1601).

Pseudo-asphodelus minor sive pumilio folio Iridis Clusius, loc. cit. (1601); Ray, *Hist. Plant.* **2**, 1194 (1688).

Pseudoasphodelus alpinus C. Bauhin, *Pinax*, 29 (1623).

Pseudo Asphodelus quibusdam J. Bauhin, Cherler & Chabraeus, *Hist. Plant. Univ.* **2**, 634 (1651) icone Pancratii excluso; Ray, *Stirp. Europ. Sylloge*, 209 (1694).

Phalangium Alpinum, palustre, Iridis folio Tournefort, *Inst. Rei Herb.* **2**, 368 (1700); Seguier, *Plant. Veron.* **2**, 61, t. 14 (1745).

Anthericum foliis ensiformibus, filamentis glabris Linn. in *Kongl. Svenska Vet. Akad. Handl.* **2**, 191 (1741).

Anthericum filamentis glabris Haller, *Enum. Stirp. Helvet.* 291 (1742).

Anthericum foliis ensiformibus, perianthiis trilobis, filamentis glabris Linn., *Öländska och Gothländska Resa*, 194, 221 (1745) as to the Gotland plant; Linn., *Fl. Suecica*, 95 (1745) as to the Gotland plant.

Anthericum calyculatum Linn., *Sp. Plant.* **1**, 311 (1753) p.p. majore, excluding Virginian, Lapland and Siberian plants; Linn., *Fl. Suecica*, 2nd ed. 107 (1755) p.p. excluding Lapland and British plants; Hudson, *Fl. Anglica*, 127 (1762) p.p. majore, the British plants.

Anthericum Pseudoasphodelus Jacquin, *Enum. Stirp. Vindobon*, 233 (1762).

Anthericum filamentis glabris Haller, *Hist. Stirp. Helvet.* **1**, 98 (1768).

Scheuchzeria Pseudo-Asphodelus (Jacq.) Scopoli, *Fl. Carniolica*, 2nd ed. **1**, 263 (1772).

Tofieldia palustris Hudson, *Fl. Anglica*, 2nd ed. 157 (1778) p.p. majore, excluding the British plant; Redouté, *Liliac.* **5**, t. 256* (1809); Sternberg & Hoppe in *Denkschr. Bot. Ges. Regensburg*, **1**, 153, t. 2, figs. *k–s** (1815); Baxter, *Brit. Phaen. Bot.* **3**, t. 227* (1837) as to plant figured.

Narthecium calyculatum (Linn.) Allioni, *Fl. Pedemont.* **2**, 165 (1785); Wahlenberg in *Kongl. Vet. Akad. Nya Handl.* **26**, 124 (1805).

Narthecium iridifolium Villars, *Hist. Plant. Dauph.* **2**, 225 (1787).

Heritera anthericoides Schrank, *Baier. Fl.* **1**, 629 (1789).

Helonias borealis Willdenow, *Caroli a Linné Sp. Plant.* **2**, 274 (1799) p.p. majore.

Narthecium alpinum Michaux, *Fl. Boreali-Amer.* **1**, 209 (1803) in obs.

Hebelia collina C. C. Gmelin, *Fl. Baden.* **2**, 117, t. 1 (1806).

Hebelia allemannica C. C. Gmelin, loc. cit. 118, t. 1 (1806) p.p. majore, excluding the Lapland plant.

Tofieldia calyculata (Linn.) Wahlenberg, *Fl. Lappon.* 90 (1812) in obs.; Billberg & Swartz, *Svensk Bot.* **7**, t. 482, fig. 1* (1812); Wahlenberg, *Veg. Clim. Helvet.* 68 (1813); Wahlenberg, *Fl. Suecica*, **1**, 225 (1824); Reichenb., *Icon. Fl. Germ.* **9**, figs. 930–33* (1848); Wiedemann & Weber, *Beschr. Gewäch. Esth-, Liv- und Curlands*, 195 (1852); Döll, *Fl. Grossherz. Baden*, **1**, 339 (1857); Kirschleger, *Fl. Alsace*, **2**, 193 (1857); Parlatore, *Fl. Ital.* **3**, 200 (1860); Willkomm & Lange, *Prodr. Fl. Hispan.* **1**, 192 (1861); Rogovich, *Oboz. Rast. Kiev*, 257 (1869); Oborny, *Fl. Mähren*, **1**, 234 (1881); St.-Lager, *Fl. Bassin Rhone*, 693 (1883); Simonkai, *Enum. Fl. Transsilv.* 534 (1886); G. Beck-Mannag. *Fl. Nieder-Österr.* **1**, 178 (1890); Herder in Engler, *Bot. Jb.* **14**, 134 (1891); Sagorski & Schneider, *Fl. Centralkarpath.* **2**, 481 (1891); E. Lehmann, *Fl. Polnisch-Livland*, 180 (1895); Pospichal, *Fl. Oesterr. Küstenl.* **1**, 216 (1897); Schmalhausen, *Fl. Sredn. Ross.* **2**, 511 (1897); G. Beck-Mannag. *Fl. Bosne, Hercegov.* **2**, 63 (1903); Ascherson & Graebner, *Synop. Mitteleurop. Fl.* **3**, 5 (1905); Coste, *Fl. France*, **3**, 297 (1905); Hegi, *Illust. Fl. Mittel-Europa*, **2**, 189, t. 58, fig. 1* (1909); Rouy & Foucaud, *Fl. France*, **12**, 465 (1910); B. Fedtschenko & Flerov, *Fl. Evrop. Ross.* 225, fig. 155 (1910); Kirchner, Loew & Schroeter, *Lebensgesch. Blütenpfl. Mitteleurop.* **1**, iii, 229 (1911); Vollmann, *Fl. Bayern*, 141 (1914); Raciborski, *Fl. Polska*, **1**, 111 (1919); Lindman, *Bild. Norden Fl.* **2**, 322, t. 395* fig. 6 (1922); Lindman, *Svensk Fanerogamfl.* 2nd ed. 172 (1926); Bonnier, *Fl. Compl. France, Suisse*, **10**, 63, t. 573* (1929); K. Krause in Engler & Prantl, *Nat. Pflanzenfam.* 2nd ed. **15***a*, 255, fig. 85 *c–e* (1930); Bertsch, *Fl. Württemberg*, 68 (1933); Kuzeneva in Komarov, *Fl. U.R.S.S.* **4**, 5 (1935); Degen, *Fl. Velebitica*, **1**, 604 (1936); Lagerberg & Holmboe, *Våre Ville Plant.* **2**, 4, t. 131* (1938).

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* Figure in colour.

Tofieldia collina (C. C. Gmelin) Schultes, *Österr. Fl.* 2nd ed. **1**, 581 (1814).

Tofieldia alpina Smith in Rees, *Cyclop.* **35** art. *Tofieldia* no. 2 (1817) et in *Trans. Linn. Soc. Lond.* **12**, 241 (1818); non Sternberg & Hoppe (1815).

?*Tofieldia stenopetala* Smith, op. cit. art. *Tofieldia* no. 3 (1817), op. cit. **12**, 243, t. 8 fig. 1 (1818).

Tofieldia rubra F. Braun in *Flora, Regensburg*, **3**, 469 (1820).

Tofieldia allemannica (C. C. Gmelin) Bluff & Fingerhuth, *Compend. Fl. Germ.* **1**, 478 (1825).

Tofieldia anthericoides Roth, *Enum. Plant. Germ.* **1**, ii, 109 (1827).

Tofieldia glacialis Gaudin, *Fl. Helvet.* **2**, 595 (1828).

Cymba calyculata (Linn.) Dulac, *Fl. Hautes-Pyrén.* 117 (1867).

Asphodeliris calyculata (Linn.) O. Kuntze, *Revis. Gen. Pl.* **2**, 706 (1891).

Restricted type-locality of *T. calyculata*, sensu stricto: Gotland (see above).

General distribution: Central European: from Pyrenees (French and Spanish) and south-eastern France (Savoy, Dauphiné, Maritime Alps) extending eastward over northern Italy, Switzerland, Austria, north-western Balkan peninsula (from Bled over the Velebit range south to Mostar in Hercegovina), Transilvania, Bohemia, Moravia to south-western European Russia (Volhynia, Chernigov, Minsk, Mogilev; cf. Schmalhausen, 1897) and northward over southern, central and north-eastern Germany (Baden, Württemberg, Bavaria and south of the line Speyer–Darmstadt–Jena–Halle–Berlin–Eberswalde–Bromberg–Tuchel–Lötzen; cf. Ascherson & Graebner, 1905), Poland, Latvia to Estonia and the Baltic islands of Moon (Muhu), Oesel (Saare Maa) and Gotland.

Tofieldia calyculata varies considerably in general size and in the form of the inflorescence, much more than *T. pusilla* does, and as long ago as 1821 Hoppe ('Aufzählung der Varietäten von *Tofieldia palustris*' in *Flora, Regensburg*, **4**, 187–90, t. 1*) described four varieties, namely, *T. palustris* α *vulgaris* (syn. *Hebelia allemannica* C. C. Gmelin), β *rubescens* (syn. *T. rubra* F. Braun), γ *capitata* and δ *collina* (syn. *Hebelia collina* C. C. Gmelin), as well as an abnormal branched state. These deserve further investigation. Gmelin's *Hebelia collina* (= *Tofieldia calyculata* var. *collina* (C. C. Gmelin) K. Richter) from Baden is a robust, lowland plant with a long inflorescence corresponding to the original *T. calyculata*; material from Karlsruhe matches closely some material from Gotland. *T. calyculata* var. *capitata* (Hoppe) Reichenbach (syn. *T. glacialis* Gaudin) is a dwarf high alpine plant, in general appearance very like *T. pusilla* but with a calyculus beneath the flower and with the leaf-tip drawn out gradually to a fine point instead of somewhat abruptly pointed as is usual in *T. pusilla*.

2. Tofieldia pusilla (Michaux) Persoon.

Asphodelus palustris Scoticus minimus Ray, *Cat. Plant Angliae*, 2nd ed. 30 (1677).

Pseudo-asphodelus palustris Scoticus minimus Ray, *Hist. Plant.* **2**, 1194 (1688); *Synop. Stirp. Brit.* 169 (1689), 2nd ed. 234 (1696).

Phalangium Scoticum, palustre, minimum, Iridis folio Tournefort, *Inst. Rei Herb.* **1**, 369 (1700); Ray, *Synop. Stirp. Brit.* 3rd ed. **2**, 375 (1724).

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* Figure in colour.

Anthericum scapo nudo capitato, filamentis glabris Linn., *Fl. Lappon.* 100, t. 10, fig. 3 (1737) p.p. majore, excluding references under α.

'*Anthericum calyculatum*' Linn., *Sp. Plant.* **1**, 311 (1753) p.p. minore, as to Lapland plant; Linn., *Fl. Suecica*, 2nd ed. 108 (1755) p.p. as to Lapland plant and var.; Hudson, *Fl. Anglica*, 127 (1762) p.p. minore, as to British plant; Lightfoot, *Fl. Scotica*, **1**, 181, t. 8 (1777); non Linn. sensu stricto.

Phalangium minimum Hill, *Brit. Herbal*, 473 (1756) nomen illegit.

'*Tofieldia palustris*' Hudson, *Fl. Anglica*, 2nd ed. **1**, 157 (1778) p.p. minore, as to British plant; Sowerby & Smith, *English Bot.* **8**, t. 536* (1799); Smith in *Trans. Linn. Soc. Lond.* **12**, 239 (1818); Baxter, *Brit. Phaen. Bot.* **3**, sub t. 227 (1837), excluding figure; Macgillivray, *Nat. Hist. Deeside*, 80, 98, 147 (1855); Baker, *N. Yorks.* 382 (1892); White, *Fl. Perth.* 293 (1898); Stefansson, *Fl. Islands*, 64, fig. 38 (1901), 2nd ed. 73, fig. 55 (1924); Ostenfeld, *Fl. Arctica*, 32 (1902); Ascherson & Graebner, *Synop. Mitteleurop. Fl.* **3**, 6 (1905); Coste, *Fl. France*, **3**, 297 cum icone (1905); Blytt & Dahl, *Handb. Norges Fl.* 204 cum icone (1906); Gray, *New Man. Bot.* ed. Fernald & Robinson, 283 (1908); Hegi, *Illust. Fl. Mittel-Europa*, **2**, 190, fig. 315 (1909); Simmons, *Revised List. Fl. N.W. Greenland* (*Rep. 2nd Norweg. Arctic Exped. 'Fram'*, **16**), 88 (1909); Porsild in *Meddel. Grønland*, **37**, 346, figs. 1, 5, 7 (1920); Lindman, *Bild. Nordens Fl.* **2**, 322, t. 395, fig. *a** (1922); Resvoll-Holmsen, *Svalbards Fl.* 34 (1927); Krylov, *Fl. Zapad. Sibir.* **3**, 583 (1929); Sørensen in *Meddel. Grønland*, **101**, iii, 165 (1933); Gelting in *Meddel. Grønland*, **101**, ii, 219 (1934); Ostenfeld & Grøntved, *Fl. Iceland and Faeroes*, 45 (1934); Kuzeneva in Komarov, *Fl. U.R.S.S.* **4**, 3 (1935); Raup in *J. Arnold Arb.* **17**, 224 (1936); Grøntved, *Vasc. Plants. Arctic N. Amer.* 31 (1936); Seitenfaden & Sørensen in *Meddel. Grønland*, **101**, iv, 107 (1937); Hultén, *Outline Hist. Arctic Boreal Biota*, 102, 127 (1937); Lagerberg & Holmboe, *Våre Ville Plant.* **2**, 4, t. 132* (1938); Lagerberg, *Svenska Fjallbl.* 142, t. 155 (1939); Porsild in *Rhodora*, **41**, 213 (1939); Polunin in *J. Bot.* **77**, 274 (1939).

'*Helonias borealis*' Willdenow, *Caroli a Linné, Sp. Plant.* **2**, 274 (1799) p.p. minore.

Narthecium pusillum Michaux, *Fl. Boreali-Amer.* **1**, 209 (1803).

Tofieldia pusilla (Michx.) Persoon, *Synop.* **1**, 39 (1805); Hylander, *Förteck. Skandinav. Växt.* **1**, 30 (1941); Stearn apud Polunin in *J. Linn. Soc. Bot.* **52**, 378 (1942); Hultén, *Fl. Alaska*, **3** (*Lunds Univ. Årsskr.* N.F. 2, **39**, i), 447 (1943); Lid, *Norsk Fl.* 43, fig. 25*b* (1944); Hylander, *Nomenkl. Stud. Nord. Gefässpfl.* (*Uppsala Univ. Årsskr.* 1945, vii), 111 (1945); J. F. Anderson, *Fl. Alaska*, **3** (*Iowa State Coll. J. Sci.* **19**, ii), 178, fig. 317 (1945); Löve, *Islenzkar Jurtir*, 114, fig. 39*e* (1945); Brit. Ecol. Soc. in *J. Ecol.* **33**, 330 (1946).

Narthecium boreale Wahlenberg in *Kongl. Vet. Akad. Nya Handl.* **26**, 124 (1805).

Tofieldia borealis (Wahlenb.) Wahlenberg, *Fl. Lappon.* 89 (1812); Billberg & Swartz, *Svensk Bot.* **7**, t. 482, fig. 2* (1812); Wahlenberg, *Fl. Suecica*, **1**, 225 (1824); Reichenbach, *Icon. Fl. Germ.* **9**, figs. 934–35* (1848); Hartman, *Handb. Skand. Fl.* 10th ed. 217 (1870); Lange, *Consp. Fl. Groenland.* **1**, 122 (1880); Macoun, *Cat. Canad. Plants*, **4**, 43 (1888); Herder in Engler, *Bot. Jb.* **14**, 134 (1891); Norman, *Norges Arktiske Fl.* **1**, 1072 (1900), **2**, 517 (1901); Rouy & Foucaud, *Fl. France*, **12**, 465 (1910); Fitch & Smith, *Illust. Brit. Fl.* 5th ed. 264, fig. 1058 (1924); Bonnier, *Fl. Compl. France, Suisse*, **10**, 63 (1929); Polunin in *J. Bot.* **72**, 204 (1934); Polunin, *Bot. Canad. E. Arctic*, **1** (Canada *Nat. Mus. Bull.* **92**), 149 (1940).

Tofieldia alpina Sternberg & Hoppe in *Denkschr. Bot. Ges. Regensburg*, **1**, 152, t. 2, figs. *a–i** (1815); non Smith (1817).

Abama pusilla (Michx.) Rafinesque, *New Fl. N. Amer.* **1**, 36 (1836).

Tofieldia capitata Rafinesque, *Autikon Bot.* 65 (1840).

Tofieldia minima (Hill) Druce in *Rep. Bot. Exch. Club Brit. Isles*, **3**, 439 (1914), nom. illegit.; Fernald in *Rhodora*, **28**, 75 (1926), **35**, 89 (1933); Marie-Victorin, *Liliifl. Québec* (*Contrib. Lab. Bot. Montréal*, **14**), 41, fig. 7 (1929); Marie-Victorin, *Fl. Laurent.* 661 (1935).

Type-locality of *T. pusilla*: Eastern Canada, near Lake Mistassini.

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* Figure in colour.

General distribution: Arctic and alpine: northern Siberia (Chukotsk peninsula, northern Yakutsk at mouth of Lena, northern Yenisei, Yamal peninsula and northern Tobolsk, Ural; cf. Krylov, 1929), northern European Russia (Archangel, Kola peninsula), northern Finland, Sweden (from Lapland to Värmland), Norway (cf. Norman, 1900–1), Scotland (highlands of Perth, Angus, Aberdeen, Banff, Argyll, Inverness and Ross, the isles of Rhum and Raasay), northern England (Upper Teesdale, on Widdy Bank in Durham and Cronkley Fell in Yorkshire), the Austrian, Swiss, Italian and French Alps (from Styria and Carinthia over Tirol and Switzerland to Piedmont, Hautes-Alpes and Savoy; cf. Hegi, 1909) and possibly the High Tatra in the Carpathians also, the Faeroes (Bordö), Iceland, western Spitsbergen (north to 79°; cf. Resvoll-Holmsen, 1927, Polunin, 1940), eastern and western Greenland (cf. Simmons, 1909; Porsild, 1920; Sørensen, 1933; Gelting, 1934; Seitenfaden & Sørensen, 1937), northern North America (Baffin Island, Labrador, Newfoundland to Alaska; cf. Michaux, 1803; Macoun, 1888; Marie-Victorin, 1929, 1935; Raup, 1931, 1934, 1936; Grøntved, 1936; Porsild, 1939; Polunin, 1940; Hultén, 1943). According to Hultén, *Fl. Aleutian Islands*, 130 (1937), reports of *T. palustris* from the Commander Islands are probably incorrect; all the specimens seen from these islands he refers to *T. coccinea* Richardson. Kuseneva (1935) records the species from the Angara-Sayan region, U.S.S.R.

Whereas *T. pusilla* of eastern Canada agrees closely with European material and is usually a very dwarf plant (though reaching 19 cm. in a specimen collected by Polunin at Churchill, Manitoba), the limited material available from western Canada (Field, B.C., *E. M. Farr*; Banff, Alberta, *W. C. McCalla*; Arctic Red River, Yukon, *R. R. Gates and K. Mellanby*) and adjacent Alaska (Forty Mile Creek, *F. Funston*) is rather taller, with flower-stems 10–27 cm. high and has more gradual acuminate leaves up to 6 cm. long. A description made from Funston's specimens is given below,[1] but more material is needed to establish whether these represent a constant variant or merely a luxuriant state.

Among the many who have helped directly or indirectly in the preparation of this article I am especially indebted to Prof. Eric Hultén for compiling the map of the distribution of *Tofieldia pusilla* (Fig. 1), which includes my data obtained from British herbaria as well as his obtained from Scandinavian and other herbaria. Fig. 2 was kindly drawn for me by Mrs V. Higgins. I am also grateful to the authorities at the Botany School, Cambridge, the Royal Botanic Gardens, Kew, the British Museum (Nat. Hist.), London, the Linnean Society of London and the Department of Botany, Oxford, as well as to the late P. A. Datton, the late Francis Druce, and Mr C. A. Weatherby for their co-operation.

Summary

The name *Anthericum calyculatum* of Linnaeus, *Species Plantarum* (1753), covered four species but was primarily based upon the central European species to which authors since 1812 have restricted the name *Tofieldia calyculata* (L.) Wahlenb. The name *T. palustris* Huds. as first published in 1778 must be regarded as a synonym of *T. calyculata*, even though it has been restricted by later authors to the circumpolar Arctic-Alpine species which alone occurs in Britain. For this the correct name is *T. pusilla* (Michx.) Pers. Linnaeus knew both species in a living state, having met with *T. pusilla* in Lapland in 1732 and *T. calyculata* on Gotland in 1741, but he did not consider them specifically distinct. The above paper summarizes the distinguishing features, history, synonymy and geographical distribution of the two species.

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[1] *Herba* perennis, glabra. *Folia* erecta vel suberecta, anguste linearia, sensim acuminata, margine minute denticulata, venis plerumque 3 interdum 4, ad 6 cm. longa. *Caulis florifer* gracilis, 12–27 cm. altus. *Racemus* cylindratus, laxus, interruptus, pauci-(10–20)florus, 1–3 cm. longus; *pedicelli* basi bractea minuta trilobata suffulti; *calyculus* nullus. *Perianthii* segmenta anguste oblongo-obovata, alba, 1·5–2 mm. longa, 0·7 mm. lata. *Staminum filamenta* alba, 1·5 mm. longa; *anthera* flava, vix 0·5 mm. longa. *Styli* vix 0·5 mm. longa. *Hab.* America borealis occidentalis: Forty Mile Creek, Alaska-Yukon boundary, 11 July 1893, *F. Funston* 121 *a* (herb. Kew).

On the origin and meaning of South American Indian potato names. By J. G. Hawkes, M.A., Ph.D.

[With 2 Sketch-maps]

[Read 8 May 1947]

Introduction

The names of some, at any rate, of the potato varieties of commerce are familiar to nearly everyone. It is little realized, however, that the original indigenous potatoes of South America are also known by special names to the Indian peasants. It is also not perhaps generally realized that the degree of diversity and the number of varieties in the Andes far exceeds the variation and number of varieties in the domestic potato of Europe and North America to-day. Probably only one or two potatoes were brought from South America to Europe in the first place, and no doubt most of our varieties were derived from these. Yet the Indian peasants often grow 50–100 separate and distinct kinds in one field alone, and taxonomists have shown that certain of these may belong to more than one botanical species.

Whilst travelling in the Andes looking for disease- and frost-resistant potatoes that might be used for crossing with our domestic types in the production of new and better potato varieties, I was struck with the complex vernacular nomenclature of these indigenous potatoes. Most of the names were in the two mountain Indian languages, Aymará and Quechua, though many were in Spanish. It seemed worth while to list them and, so far as was possible, to translate them into English, in the hope of finding out more about the origin and uses of the potatoes to which they were applied. Furthermore, since many potato breeders are using the material collected by the author and his colleagues, Mr E. K. Balls and Dr W. B. Gourlay,[1] and are at once confused and astounded by the curious names that the varieties bear, it was felt that some sort of explanation of these words that to us seem so exotic and apparently unpronounceable was warranted. The task would certainly not have been attempted had the author known of anyone more competent to deal with a subject for which he himself was not trained, and it is therefore with some trepidation that he ventures to present the following account.

Whilst engaged on the work of translating the varietal names of the different *sorts* of potatoes, it became evident that in order to present a more logical and comprehensive account it would be necessary to begin with a study of the name of the potato itself in the Andes and other regions of South America where it was cultivated by the Indians prior to the Spanish conquest. This forms the second portion of the present work (the first part being concerned with the languages themselves and the methods of transliteration) and has been largely obtained from dictionaries, vocabularies and other written records, supplemented by the writer's own observations when in South America. In this portion the writer has attempted to trace the name of the potato in every language where records of it exist. In the third part of the paper, however, when dealing with the overwhelmingly prolific number of varietal names, the author has thought it better to confine himself to names of potato varieties that he either personally collected or has grown at Cambridge from living material sent from South America after his return. In this way it was possible to be quite sure that a certain name was in use at the present day, and to possess accurate information on the region of South America where the potato to which it was applied was cultivated.

The author wishes to express his very grateful thanks to Dr Martin Cárdenas, Rector of Cochabamba University, Bolivia, for checking through and correcting all the Quechua and many of the Aymará words and for offering many useful suggestions as to their possible meaning. His thanks are due also to Dr R. N. Salaman and to Mr G. H. S. Bushnell for carefully reading through the manuscript and giving much useful advice and criticism.

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[1] The potatoes were collected on an expedition sent out by the Imperial Agricultural Bureaux from Cambridge, England. Detailed accounts have already appeared (Hawkes, 1941, 1944).

Part I. The linguistic problem

In the present study it is not intended to deal with the many Spanish potato names that are found in South America, since these may easily be translated with the aid of a Spanish dictionary and in general are only of recent application.

The Aymará and Quechua names, on the other hand, are often of very ancient usage, and certain classes of potatoes mentioned by Bertonio in his *Dictionary of Aymará*, published in 1612, are still in use at the present day.

At the time of the conquest the Quechua language, which was the official tongue of the Inca empire, extended in the Andes from north Ecuador to north Argentina and north Chile (see map 2), but although the Aymará Indians had been conquered at about the beginning of the twelfth century A.D., they still retained their own language when the country was discovered by the Spanish, and do so to this day. The Aymará Indians are generally considered to have developed their civilization at an earlier period than that of the Incas who conquered them and adopted many of their words, though the two languages are fairly distinct. Some authorities, however, consider that Aymará was the parent tongue and that Quechua is derived from it though altered almost completely by the assimilation of words from other Indian tribes which the Incas conquered.

There is little doubt that the potato was a very important and ancient crop amongst the Aymarás, as evidence the very large number of words for it listed in Bertonio's dictionary and for the cultivation processes in connexion with it. Hence, a study of the names in this language, even more than in Quechua, might give some indication of the origin of the potato varieties to which they are applied, as Dr V. Lechnovicz of Leningrad (in a personal communication) considers possible. In surveying the lists of words at my disposal I have not, however, been able to find any words that give very definite clues to the origin of the potato itself or of its varieties, though one or two possibilities will be examined later. The chief difficulties to a study of this kind are the lack of dictionaries, no complete dictionary of Aymará having been published since that of Bertonio in 1612. There are rather more dictionaries of Quechua, though none of them are by any means exhaustive. As to any languages other than Quechua and Aymará, although short lists have been published by certain authors, no good dictionaries have been available to the writer, except for Chibcha in Colombia and Araucanian in Chile.

The two better-known native languages also present great difficulties in transliteration, since a large number of explosive and aspirated sounds are present which have no exact equivalent in Spanish or any other European language. Neither Quechua nor Aymará possessed any written characters before the advent of the Spaniards, so that the work of transliteration into Roman characters of these unusual sounds presents a work of great difficulty. The explosive sounds have been represented by most authors by doubled consonants, whilst an extra *h* was added when they were to be aspirated. Other lexicographers, perhaps more ingeniously, made crescent-shaped hooks, placed before or after the letter according to whether it was to be aspirated or used explosively respectively. Middendorf's dictionaries (1890, 1891, 1892) are written in this way. Others again, such as that of von Tschudi (1853), placed curved lines across the uprights or tails of the letters when an alteration of the sound was needed.

This confusion of transliteration has naturally rendered the task of translating the potato names extremely difficult, since a slight change in the spelling in some directions can alter the sense of a word completely, whilst in other cases completely differing spellings can be attached to one and the same word. In a work of this sort one can only begin, in the absence of any accepted usage, by setting down the method to be used in the present work together with the approximate equivalents to the combinations of letters used by previous authors. Although Aymará is said to be a much more guttural language than Quechua it can generally be written with the same conventions.

In both languages the consonants B, D, F, G, V, X and Z are altogether wanting. The *w* sound is present in Quechua and Aymará but is absent in Spanish, so that it has generally been the convention to represent it by the combination *hu*, since this was always done in the first dictionaries compiled by the Spaniards. In Ecuador and Colombia this sound is generally written *gu*, and it is possible that it may actually be pronounced more like *gw* than *w*, though the present author could detect little difference when in these countries.

The vowels *a*, *e*, *i*, *o* and *u* are more or less as in Spanish and are said to be generally pure sounds. Nevertheless, the *u* sound seems to be pronounced half-way between the Spanish *o* and *u*, so that it is often written as an *o* by the Spaniards. Many authors also use *y* instead of *i*, especially at the beginning of words, since in Spanish these two letters are pronounced more or less the same.

The diphthongs *au*, *ao*, *ai*, *ei*, *eu*, *ua* and *ui* are also pronounced as in Spanish.

It will probably be best to represent the consonants in a table, giving the equivalents of previous authors and the approximate pronunciation.

TABLE 1. *Pronunciation of the consonants in Quechua and Aymará*

Present work	Modern Spanish	Middendorf	Approximate pronunciation
c	*c*	*c*	Hard, as in English; replaced by *qu* before *e* or *i*. Sometimes replaced by *g*, especially with the older Spanish authors
ch	*ch*	*ch*	Pronounced as in 'church'
	chh	*'ch*	Rather more aspirated
	cch	*ch'*	Rather more explosive According to Cárdenas the differences between these three sounds are slight and might be neglected for the purposes of the present work
ck	*ck, cj*	*'k*	Pronounced as a strongly aspirated or rather guttural *k*. Sometimes also written as *g*
hu	*hu*	*hu*	As the English *w*
j	*j, h*	*j, 'h*	As the English *h* but more gutturally
k	*c, cc*	*k*	As *c* but rather more strongly. Many authors do not recognize the difference between *c* and *k*
kk	*cc*	*k'*	Pronounced very explosively. If rendered as *cc* it is replaced by *qqu* or *ququ* before *e* or *i*
l	*l*	*l*	As in English
ll	*ll*	*ll*	As *lli* in 'million'. This letter is often pronounced as *y* in 'yacht', and the sound is therefore sometimes seen written as *y* instead of *ll*
m	*m*	*m*	As in English
n	*n*	*n*	As in English
ñ	*ñ*	*ñ*	As *ny* in 'canyon'
p	*p*	*p*	As in English
pf	*ph, pf*	*'p*	Pronounced like a *p* with a faint *f* or *h* after it. It was thought better not to use the *ph* combination, since in several languages this is pronounced as *f*, a sound that does not occur in Quechua or Aymará
pp	*pp*	*p'*	Pronounced very explosively
qu	*qu*	*qu*	Before *e* or *i* only; pronounced as *c* above
r	*r*	*r*	Well pronounced, as in Spanish
s	*s*	*s*	Hissingly; sometimes written *ss*
t	*t*	*t*	As in English
th	*th*	*'t*	As in 'think', not as in 'though'
tt	*tt*	*t'*	Pronounced very explosively

PART II. THE INDIAN NAMES FOR THE POTATO

(1) *The cultivated potato*

Before dealing with the many varietal names given to the potato it will be of interest to inquire into the general names for potatoes among the American Indians who cultivated them.

The most widespread word is *papa*. This is accepted by most as a Quechua word that was carried by the Quechua-speaking Incas through the whole range of their empire from southern Colombia to northern Chile. It was a word mentioned by all the earliest chroniclers as specifically applied to the plant which was previously unknown to them and which we to-day call the potato. The Spaniards therefore took this word into their own language, introducing it into other regions where it was previously unknown. It is in general use in South America and in parts of Spain at the present day.[1]

Cieza de León (1553), one of the first Europeans to mention this newly discovered root, mentions *papa* several times, both at Quito, where he first saw the plant cultivated and again in the highlands of Peru. Speaking of the Quito Indians he says: 'Of provisions besides maize, there are two other products which form the principal food of these Indians. One is called *papa* and is a kind of earth nut, which after it has been boiled is as tender as a cooked chestnut, but it has no more skin than a truffle and it grows under the earth in the same way.' Similarly, with the Peruvian Indians: 'Their principal food is *papas* which are like unto earth nuts, as I have before described.'

The Inca Garcilasso de la Vega, a person of mixed Inca and Spanish blood with a deep knowledge of the habits and customs of his Indian ancestors, states in his *Royal Commentaries* (1609): 'Besides the maize lands which were irrigated, other unirrigated tracts were portioned out, in which they sowed other crops of much importance, such as those they call *papas*, *ocas*, and *añus*'; and again, speaking of the crops grown in the mountains or Colla: 'Among these there is one called the *papa*, round and moist, and inclined to rot soon on account of its moistness.' Further on: 'The most important [crop] is the *papa* which serves them instead of bread. They eat it boiled and roasted, and also in their stewed dishes.'

Father Acosta, who travelled in Peru for some seventeen years, also mentions the word *papa* in his *Natural and Moral History of the Indies*, published in 1590. Thus: '. . .yet the want they have of bread is countervailed with the rootes they sowe, the which they call *papas*, and they grow in the earth. This plant is the Indian's food.'

Papas are also mentioned by Zárate in a work published in 1555, *History of the Discovery and Conquest of the Province of Peru*, and by Vázquez de Espinosa (1629); by Felipe Guamán Poma de Ayala (1583–1613), Cristóbal de Molina (1570–84) and by Polo de Ondegardo (*c.* 1560).

In one of the earliest known dictionaries of Quechua written by Gonçalez Holguín (1586), who lived and studied for more than 25 years in Cuzco, the ancient capital of the Incas, we find: 'Papa: Rayzes de comer que siruen de pan como turmas de tierra.'[2] Holguín also gives several combinations of other Quechua words with *papa*, explaining the meaning of certain words connected with its storage and preparation for the table.

The European Herbalists also, who were sent this new root and gave it its first botanical description, had the name *papa*, all of them attributing the word to the language of the Indians who grew it.

We have dealt with the word *papa* at some length and have purposely multiplied the examples of its occurrence in the oldest records with a definite end in view, namely, that of attempting to refute the statement made by certain writers that the word was not indigenous to South America. Mitchell (1886), for example, states (p. 583): '...it should be remarked that there is a possibility...that *papas* may have become a common name for a root good to eat, derived from that universal sound infants make when wanting food, in which mothers recognize the properly articulated word.'

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[1] In Velázquez, M. (1900) we find: 'Papa (Provinces, and America)—The potato.' Dr R. N. Salaman tells the writer that 'papa' is used in the provinces of Estremadura and Andalucia.

[2] Edible roots used in place of bread, like truffles.

W. F. Wight, in a work written in 1916 entitled, *Origin, Introduction and Primitive Culture of the Potato*, though mentioning the fact that certain opinions are against the Indian origin of this word, inclines on the whole to consider it truly indigenous. He states: 'It has been contended that the word is nothing more than an adaptation of the old Latin word *papa* meaning nourishment of any kind, and having its origin in the sound infants make on demanding food, and that the Spanish on finding the potato extensively used for nourishment, applied this word to it. That from this use by the Spanish it was adopted by the Indians and became almost, if not quite, universally applied in South America.

'Some Europeans resident in Peru who have been more or less engaged in scientific work are of this view and I was assured by a Quechua Indian who had received a University training abroad and who was the most cultured Indian I met, that the word positively did not belong to his native language.' Wight then goes on to question whether the opinions of such men who represent a race that has lived under Spanish domination for 350 years can carry much weight in an argument of this kind.

The evidence presented above from the earliest accounts of the chroniclers and lexicographers would seem to be irrefutable; the word *papa* must surely be truly indigenous, since these men were among the first Europeans to come into contact with the Indians and could at first only converse with them by means of interpreters. Is it possible that the Spanish influence could have spread so rapidly as to supplant the Indians' own word by a meaningless one of alien sound? On the contrary, the Indians throughout the whole post-conquest period have clung stubbornly to their customs and language, as every student of the subject will readily admit. One cannot avoid the conclusion that if the potato was indigenous to these regions at the time of the conquest, and no one would dispute this fact, then its name must have been indigenous also.

Furthermore, in those areas that had not been brought under the domination of the Inca empire at the time of the Spanish conquest and had therefore not been forced to adopt the Quechua tongue, the word *papa* was not in use in the early days, since the inhabitants of these regions had their own name for the potato, as we shall see below. The two chief areas where the potato was cultivated indigenously but which had not been conquered by the Incas were Colombia and Chile. When *papa* had been adopted into Spanish it gradually supplanted the original names in these countries when the indigenous languages had died out; but in the days of the conquest and in Chile for several centuries afterwards there is evidence to show that the word *papa* was not used. It is therefore fairly obvious that *papa* was not a word introduced by the Spaniards, since had it been so it would have been found in these two countries right from early colonial days as it was in Peru.

Again, if we concede, for the purposes of the argument, that *papa* was a Spanish word, we should expect to find the old Quechua word for it in addition, at any rate in the older dictionaries. But in Quechua there is no other word for it if we except the northern dialect word *ajsu* (see below, p. 211), and it seems therefore from this point of view most reasonable to conclude that *papa* was the original and non-Spanish word.

Yet, though the evidence presented above is very much in favour of the word *papa* being indigenous to the Quechua language, rather than to the Spanish, there is certain other evidence to show that the Indian mentioned by Wight may not have been altogether wrong. Dr Mártin Cárdenas, to whom the author is indebted for much detailed information in the present work and who has an excellent knowledge of Quechua, is also of the opinion that the word *papa* is not strictly Quechua in sound. This, however, does not render it necessary for us to revert to the hypothesis of the Spanish origin of this word, and in any case we have shown fairly conclusively that this latter hypothesis is untenable. In my opinion the solution of the problem is to be sought in other directions.

It is known, for example, that the Incas conquered and absorbed many tribes during the 400 years[1] of active colonization from the valley of their capital city, Cuzco. It might be possible that the word was borrowed from some conquered Indian tribe which became completely absorbed into the Inca empire and whose language, but for a few words that were taken into Quechua, completely died out. One may even concede that the word is onomatopoeic, one of the fundamental utterances of young infants, which is in many European languages identified with the word 'father', whilst in certain Amazonian tongues the word *papa* may mean 'mother' or in many tongues 'father'. Thus in Chiquita *papa* = mother (Adam & Henry, 1880), whilst according to Crevaux, Sagot & Adam (1882) the word *papa* means father in Roucouyenne and Galibi, both languages of the Guiana Indians. Coudreau (1892) also mentions *papa* = father in the Guiana Indian languages Ouayana, Aparaï, Oyampi and Émérillon. The author has not been able to find the use of the word in the same connexion in the languages of the Indians nearer to the Andes, though the Chiquita Indians inhabit the Vera Cruz region of eastern Bolivia; it is, however, possible that it might have occurred in cognate languages nearer to the regions that the Incas conquered, or, as was postulated above, to have been taken into Quechua from the language of some conquered tribe. Here is a problem that the competent etymologist might have little difficulty in solving. One piece of evidence that may or may not be of value in tracing the derivation of *papa* comes from the language of the Chimu Indians (see Map 1). The Chimu or Mujik civilization of the coastal regions of north Peru is known to antedate that of the Incas and was conquered by them at about the end of the fourteenth century A.D. Their language did not completely die out, however. Yuncan or Yungan, the language of the Chimu or Mujik (Muchik) peoples, was still apparently current enough for Middendorf (1892) to be able to construct a grammar and vocabulary. In this he gives the name for potato as *papa*, so that it is tempting to assume that it was a Yuncan word borrowed by the Quechuas when they conquered the Chimus. But we must consider that, without further confirmatory evidence, the word might on the contrary quite well have been borrowed by the Chimus from the Quechuas, rather than the other way round. Here again the help of the etymologist is badly needed.

Mejía Xesspe (1931), quoting from an unpublished work by Tello on the Akkaro or Kauki language, also gives *papa* = potato. No reference is given as to the area in which this language is spoken, but it is probable that it is close to if not confluent with the Quechua-speaking area, since many words in the list seem to be borrowed from Quechua or Aymará, the word *papa* included, probably.

We thus have only very slight indications and for the rest a certain amount of negative evidence for the derivation of the word. Further research in this quarter is needed before the problem can be resolved.

In the experience of the writer from his travels in South America the word *papa* may, in addition to its narrower meaning, be used in a broader sense to denote any sort of underground tubers, not only those of *Solanum* (sect. Tuberarium) species. Especially with the wild forms this word is almost if not exactly identical in meaning with the word 'tuber'. Thus, when asking to be shown wild potatoes (*papas silvestres*), the author and his colleagues would be taken by the average Indian possibly to wild tuberiferous *Bomarea* or *Verbena* plants. 'Una papa silvestre que parece una papa cultivada' (a wild potato almost similar to a cultivated one) narrowed down their conception to the tuber-bearing Solanums. Cultivated tubers other than potatoes, however, are not called *papa* but have each their own special name. These will be dealt with below (pp. 219–21).

We have seen above that the word *papa* was in general use among the Quechua-speaking Indians at the time of the conquest and was also current in Yuncan, the language of the

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[1] Some authorities would shorten this period considerably. However, the Inca colonial period was certainly not longer than 400 years.

Chimus in 1892 when Middendorf published his dictionary of that tongue. Nevertheless, this is not the only indigenous word for potato in South America, even in the regions conquered by the Incas where Quechua was the official language. At least three, probably more, other names from the languages of the conquered peoples were in current use in the period immediately subsequent to the Spanish conquest, and one of these has survived up to the present day. This survival has in consequence caused not a little confusion among those European authors who have been concerned with the potato in South America from certain other aspects, and are somewhat unfamiliar with the indigenous American languages.

The first of these Quechua dialect words we shall mention is *ajsu* (also spelt *acsu* or *akshu*). Confusion has arisen over this word, since, according to most authorities, it belonged to the Chinchaysuyo and Chanca dialect. Chinchaysuyo was the north central region of the Inca empire comprising the present Peruvian department of Junín, but not including the Yuncan region of north Peru or the area that comprises present-day Ecuador.

In a vocabulary of the Chinchaysuyo language (1603), Jean de Figueredo mentions the word *acsu* = papas. Markham (1864), however, gives *acsu* = petticoat and *ascu* = papa, potato. According to Wight, the word *ascu* does not appear in any vocabulary except that of Markham, and he is of the opinion that Markham is in error. The present author also has not been able to find it. The vocabularies and dictionaries of Quechua, such as that of Gonçalez Holguín (1586), Antonio Ricardo (1586) and others were all written in the Cuzco district which is south of the region where the Chinchaysuyo dialect was spoken; their word *acsu* = petticoat was obviously a normal Quechua one with no connexion with the dialect word *acsu* = potato. More modern lexicographers such as Middendorf give the spelling as *ajsu* (the *j* sound here apparently is so hard as almost to approximate to that of a *c*) and define it as 'a kind of shirt without sleeves or collar finely woven from wool or cotton'; but Middendorf also gives *ajsu* (department Junín [i.e. the region of the Chinchaysuyo]) = a kind of potato. Mejía Xesspe (1931), in his work on the food plants of the Indians, also mentions the word but with a slightly different spelling: 'Papa o patata = *papa, akshu.*'

On the whole it seems fairly safe to assume, therefore, that *ajsu* (*acsu*, *akshu*) was the Chinchaysuyo word for potato and that Markham made a slight mistake in the spelling. It is further probable that the word has become obsolete at the present day, though this would need confirmation. I did not encounter the word in central Peru, but there is a possibility that it might be current farther north where fewer travellers penetrate. Certainly, one is probably fairly justified in presuming that Mejía obtained it from a source other than the standard dictionaries since he gives a slight variant to the spelling.[1]

It is worth noting in passing, that Figueredo (1603) also mentions a word *achachan* as being equivalent to *papa*. This, however, may very probably be applied to *Oca* (q.v. below, p. 220) when prepared for food in a special way and not to potatoes.

The Anti or Campa race of Indians inhabited a part of Peru very close to Cuzco and were early conquered by the Incas. Their district comprised the region between the rivers Apurímac and the Quillabamba-Santa-Ana just north of Cuzco, and was known as Antisuyo. Their language must have died out very soon after the Spanish conquest. Probably even then it existed only as a local dialect, with Quechua as the main tongue. Fortunately, a manuscript by an unknown author giving grammar and vocabularies was found by M. Charles Leclerc at Toledo and published by him in 1890. From the vocabulary in this volume there are at least four words for potato (*papas*): *impari*, *maona*, *mutza* and *zanaro*. In addition the word *catzari* is given for 'papas de la sierra', which can probably be translated here as wild potatoes, since the same type of definition is found sometimes in Quechua according to Cárdenas (personal communication) and means potatoes that grow in the wild mountainous regions. So far as the present writer is aware these words from the Anti language have not been adopted into Quechua, or at any rate are not in use at the present day.

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[1] In a collection of potatoes recently received from Peru there were no less than four varieties with names containing the word *ajsu* (here spelt *acczu*; the names were *Puca a.*, *Mascca a.*, *Suito a.* and *Yana a.*). Unfortunately, the exact provenance of these samples was not given, but since they occurred in the same sequence as other potatoes whose names indicated that they came from Central Peru, and since most of the samples seemed to be arranged geographically, it can be tentatively assumed that these varieties were also from Central Peru. It seems, therefore, just possible that the name *ajsu* (or *acczu*) still lingers on in varietal combinations in Central Peru, as we shall see later in the case of *poñi* in Chile.

In the early days of their wars of conquest, though at a period later than the time when they subdued the Antis, the Incas spread southwards from Cuzco towards Lake Titicaca and into what is now the present state of Bolivia. This region, named by the Incas Collaysuyo, was inhabited by a race of Indians speaking a language known as Aymará. These peoples were probably already well versed in potato culture, since their language is rich in words connected with this plant.[1]

The Aymará Indians had two words for the potato, *choke* (also spelt *cchoqque*, *choque*, etc.) and *amka* (also rendered as *amcca*, *amkha*, etc.). These Indians have retained their language to the present day, and the former word may very frequently be met with by the potato collector. It is possible that at one time *amka* may have signified potato in a general connotation whilst *choke* indicated rather the raw potato[2] in contradistinction to the cooked one which was known as *kcati* (see p. 247). In my own experience, however, the word *amka* seems to have died out, since I did not encounter it when in Bolivia; and though it was mentioned by Bertonio (1612), García (1917), Markham (1908), and Mejía Xesspe (1931), the later authors may very well have borrowed it from Bertonio. The word may, indeed, be quite obsolete, since I have not been able to find mention of it in any lists made by collectors and field investigators, though *choke* is of very frequent occurrence in the Aymará-speaking districts of Bolivia. Bertonio's definition of both words is 'Comida ordinaria de los Indios' (ordinary food of the Indians). I encountered the word *choke* eight times, generally in combination with the word *ppitu* (=toasted maize flour). These sorts were bitter and were also known as *luki*.

The potato was cultivated to a wider extent than the confines of the Inca empire, and, as one might expect, it received a name in the Indian languages indigenous to the areas in which it was grown. Thus the Yuracare or Yurajure Indians, who inhabited the lower lying valley regions of the eastern Bolivian Andes and who probably were not brought under Inca dominion, have various words for potatoes: 'Papas que se crian por acá (potatoes that are grown hereabouts)—*cotohue*, *cuinire*, *obe*, *puspu*, *pospo*, *some*' (La Cueva, 1893). Are we to assume that these names all refer to the genuine wild or to the cultivated potato? We do not know, but it is possible that in actual fact they apply to the tubers of other plants, since the region inhabited by these Indians would be possibly too low for potato cultivation (see Map 1).

Another bordering tribe of Indians that may not have been completely under the dominance of the Quechua-speaking Incas at the time of the Spanish conquest were the Páez Indians of Colombia. These peoples inhabited the central Cordillera in what is now the department of Cauca, and must certainly have been to some extent vassals of the Incas, since in Uricoechea's *Vocabulario Páez-Castellano* (1877) we find the following definition: 'Papas, turma de tierra—*caca*.' This author, however, considers it to be a Quechua word, but thinks that it might be a Páez word originally and have been derived from the tax that the Páeces paid to the Peruvians in a product natural to their country.[3] Certainly it is more than likely that the potato was a frequent article of food among these Indians, since the high, cold regions of the Cordillera de Guanácas where they chiefly lived were called the Páramo de las Papas. Some authors, however, consider that they lived more to the north of this region.

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[1] Bertonio, writing in 1612, gives in his dictionary a list of twenty-three different types of potato in addition to many other words and phrases in connexion with their cultivation.

[2] *Choque*=raw, crude (*Ay. Cat.* 1894; Forbes, 1870); =raw potato (Markham, 1864).

[3] 'Esta voz me parece quechua: *Kaca* significa en dicha lengua víveres de contribución: o tal vez haya pasado al quechua de la lengua páez por la contribución que a los peruanos pagarían los páeces en un producto natural de Colombia' (Uricoechea).

I am indebted to Mr G. H. S. Bushnell for kindly drawing my attention to a reference to the potato in Ecuador by Sr Jijón y Caamaño (1919). This author states that the Colorado Indians of north-west Ecuador (Province Esmeraldas) give it the name *pulu*. In the nearly related Cayapa tongue from the same province there comes the similar word *pulyu*, according to Barrett (1925). One does not know, however, to what extent these names are in current use.

A lesser empire than that of the Incas, but one which was growing rapidly and but for the Spanish conquest would have soon reached the borders of the Inca domains, was that of the Chibcha Indians in central Colombia. Their chief town was Bogotá, the present capital of Colombia. The language has to-day almost died out, at any rate in the more populated regions, but several vocabularies are extant, and from one compiled by Uricoechea (1871) on the basis of certain ancient manuscripts we extract the following:

Papa, truffle: *iomza, iomuy.*
Yellow potato: *tyba iomy.*
Narrow potato: *gaza iomy.*
Floury potato: *guyhysa iomy*
White potato: *xie iomy.*
Large potato: *pcuaso iomy.*
Long potato: *quy iomy.*
Very small potato: *iomzagá.*
Black potato: *funza iomy.*
Potato with black flesh: *bhoxio iomy.*

This list indicates not only that the potato had a definite name in the Chibcha language, but that many different sorts were cultivated in Colombia even in early days.

So far as I was able to ascertain when in Colombia the name *iomy*, *iomza*, or *iomuy* has now been completely superseded by *papa*, though according to Uricoechea (1871, p. 208) it was still in use up to 1871 in the Bogotá region in the derivative word *iomogó* (*iomgo*), signifying the part of the potato harvest that is apportioned to those who help to gather it. The author also gives the word *futearse*, derived from *afutynsuca*, meaning to rot or become rotten, specifically applied to potatoes. Possibly other Chibcha potato words still linger in the more remote regions or have been assimilated into the local dialects. In any case it would be of great interest to ascertain whether the two words mentioned by Uricoechea as in use in 1871 are still current.

Finally, we have to deal with the name given to the cultivated potato by the Araucanian Indians of Chile.

Probably the first mention is by Padre Luis de Valdivia in a vocabulary published in Lima in 1606. In this he gives the word *poñu=papas*, and this is presumably the first reference to the potato in Chile. The next mention is by P. Andrés Febrés in his *Diccionario Araucan-Español*, published in Lima in 1765. On p. 199 we read *poñi* or *poñu=papas*. Molina (1787) mentions the word *poñi* (spelt *pogny*, since the work was originally written in Italian), but apparently at this time *papa* was considered as an alternative name. The word *poñi* is also mentioned by Claude Gay (1865) and by La Grasserie (1898), but it is possible that these authors may have it merely on the authority of Molina and the earlier writers and have not actually verified it from first-hand experience.

It has been considered likely by some writers that *poñi* has now become completely obsolete and was in any case never of universal application. Thus Wight (1916): 'When talking among themselves perhaps the Indians once used the word "poñi", or possibly they once used it and it has now disappeared; however that may be, I did not once hear the word applied to the cultivated potato though I spent several weeks among them and traversed the region lying between the northern limit of the Araucanian country and latitude 43° south, and between the Pacific and the Argentine boundary.' However, he continues in the next paragraph that the name was 'in use in the province of Concepción among the natives' in 1714, though we are not given the authority for this statement.

I have not been in a position to obtain a great deal of the present-day literature on the potato in Chile, so that it is a matter of some difficulty to decide whether the word *poñi* is still in wide use. Señor R. Opazo, in the chapter dealing with potatoes in his book *Agricultura*, published in Santiago de Chile in 1939, throws a certain amount of light on the problem. After stating (probably on the authority of Molina?) that the name *poñi* was used by the Araucanians, he mentions that in Atacama the potato is called *chusli*. This word is new to the literature of potato names and does not seem to be of Quechua derivation. In view of the fact that the Atacama region is almost entirely desert and would never have supported indigenous potato cultivation, even if it does so now, it is more reasonable to suppose that the word *chusli* is applied to some other tuberiferous plant quite unrelated to the potato. Further confirmation or refutation of this name is necessary before we can decide whether it was actually applied to the potato.

Of great interest, however, in connexion with Wight's statement quoted above, is that among a list of potato varieties given by Sr Opazo which are stated to be grown in Chiloé at the present time we find the names *quentrepoñi* and *parturi-poñi*. We are thus certain that in Chiloé at any rate the word *poñi* has not yet completely died out, even though it is not in such general use as *papa*.

It will probably be of use at this stage to summarize the information on the names for the cultivated potato in the various Indian languages with which we have dealt. They are therefore listed in Table 2.

TABLE 2. *The American Indian names of the cultivated potato*

Name	Language	Region
Papa	Quechua	South America. Originally confined to the Cuzco district of Peru, and later spreading with the spread of the Inca empire
Papa	Yunga (probably derived from Quechua)	Peru, departments Piura, Ancash, Trujillo, Lambayeque
Papa	Akkaro or Kauki	?
Ajsu	Chinchaysuyo	Peru, department Junín
Impari	Anti	Peru, just north of Cuzco
Maona		
Mutza		
Zanaro		
Amka	Aymará	Lake Titicaca and La Paz districts
Choke		
Cotohue	Yuracare	Bolivia, eastern valley regions
Cuinire		
Obe		
Pospo		
Puspu		
Some		
Pulu	Colorado, Cayapa	Ecuador, province Esmeraldas
Pulyu		
Caca	Páez	Colombia, department Cauca
Iomza	Chibcha	Colombia, central and northern regions
Iomy		
Iomuy		
Poñi	Araucanian	Chile, central and southern regions to the Isle of Chiloé

Summing up this section we are forced to the rather disappointing conclusion that although many fresh words for the potato have been brought together for the first time from old and new sources and its name has been traced in not a few of the Andean Indian languages and those from adjacent regions, we are still no further towards discovering the source of the word *papa* or any other of the names mentioned above than we were to begin with. Furthermore, owing to this lack of information as to its derivation we can obtain no idea on the origin of the plant itself. Had it been possible, for instance, to point to a name similar to *papa* in the language of a certain tribe that was known to pre-date Quechua-speakers then we could fairly legitimately have drawn the conclusion that it was in this region, or in some other if the word could be traced farther back still, that the potato was first brought into cultivation. No such evidence has yet been found, with perhaps the doubtful exception of the Chimu or Yungan word for potato that is identical with the Quechua word, and we can only say that perhaps a further study may yield some more useful evidence of the type mentioned above.

(2) *The wild potato*

The various names given by the South American Indians to the wild potato are generally descriptive of their conception of the wild plant in relation to the cultivated one. For the most part the wild potato is considered to be an escaped and degenerated cultivated potato. Further, the potatoes that are left behind in the soil after harvest and produce new plants next year, known to us as 'ground-keepers', are also confused with wild potatoes in many cases, since, if one believes as the Indians do that all wild potatoes are escapes from cultivation, then the ground-keeper is obviously of the same nature, not perhaps very much degenerated as yet, but nevertheless of the same category as the other potatoes growing outside his fields. The so-called degeneration idea of the potato is reflected, too, in the names given to certain weed potatoes. Here we find, for example, such names as 'fox potato', 'bird potato' or 'dog potato', used in much the same sense as we should use the phrase 'dog latin', indicating something degenerated or debased.

A further stage removed is the truly wild potato that grows far from human habitation. This, the Indians think, was cultivated in long ages past by their ancestors who once lived in these regions, which have now reverted to wild or bush country. Other wild potatoes are named merely from the regions in which they are to be found; in this class of names are to be found 'bush potato', 'mountain potato', etc., the latter word indicating that the potatoes are found in wild, uncultivated, mountainous regions. Of particular interest in this respect is the fact that several cultivated species, notably *Solanum curtilobum* and *S. Juzepczukii*, that are considered on taxonomic and genetical grounds to have been formed as natural hybrids between the wild species *S. acaule* and some cultivated species such as *S. stenotomum* and *S. andigenum* (see Hawkes, 1944, pp. 73, 100), also bear varietal names indicative of their wild affinities such as *Orkko*, *Mallcu* and *Ruqui*. The Indians apparently recognize the wild characteristics of these species and apply to them names which give some indication of their origins. We shall return to this subject later (see Table 4).

In Mexico, wild potatoes are without exception given the Spanish name *cimarrona*. This word merely means wild, or, literally, escaped. No Indian or Aztec words are used, so far as I am aware, to describe any wild potato variety in that country, whilst of course the cultivated potato was not known there before the advent of the *conquistadores*.

There is little of interest, either, from Colombia or Ecuador, though a certain number of words have been found and are included in Table 3. The second column of this table indicates whether the name was obtained by the author from samples collected by him in South America or has been obtained from vocabularies and dictionaries. The sources for the *translation* of these words will be found on referring to Table 8 et seq.[1]

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[1] I had intended to include in each table the botanical name of the potato to which the native name was applied. This task, however, proved to be impossible, chiefly for the fundamental reason that Indians name their potatoes on tuber characters and the tubers of wild potatoes all look almost identical. The different names for wild potatoes in any one language or district are based more on differences of habitat or, as we have seen above, on the estimation of how far the potato is considered as an escape from cultivation rather than on constant varietal or specific differences.

TABLE 3. *Names of wild potatoes in Ecuador and Colombia*

Word	Source	Notes	Locality
Chava	J.G.H.	A weed or semi-cultivated potato	Lake Tota, central Colombia
Ihua, Igua	Tascón	‘Potatoes that grow from those left behind at harvest’	Colombia
Achspa	J.G.H.	Wild potato	Pichincha, Ecuador
Chigua, Chihua	J.G.H.	Wild potato, named presumably after the fruit of *Zamia chigua*. This is a Cicadaceous plant with edible fruits, according to Tascón	South Ecuador
Zhio	J.G.H.	Spontaneous in cultivation, ?= ‘ground-keeper’	Azogues, south Ecuador
Sacha papa	J.G.H.	*Sacha* literally=tree, but in this connexion *sacha papa*=jungle, scrub or bush potato	Pichincha, north Ecuador

The list of words from Colombia and Ecuador in Table 3 contains one definitely Quechua word, *sacha*; two that are used in Quechua but may have been borrowed from the Indian languages of the regions in which they occur, *ihua* and *chihua*; and three words, *chava*, *aschpa* and *zhio*, whose exact meaning and language of origin is unknown. It is possible that the Colombian names may be taken from Chibcha and the Ecuadorian ones from Quito, Cañarian or Yuncan.

In Peru and Bolivia there is less doubt as to the original language of the words for wild potato and naturally the majority belong to the Quechuan tongue. In Table 4 we shall give an alphabetical list of the Quechua words encountered in these two countries; as in Table 3, column 2 indicates the source for the word, not for its translation. Column 4 indicates to what type, *in my opinion*,[1] the potato belongs, e.g. C=cultivated potato with wild characteristics; G.=‘groundkeeper’, i.e. potatoes growing from tubers left behind from the last harvest; S.=semi-wild or weed potato; W.=truly wild potato.

We have already mentioned (p. 212) when dealing with the cultivated potato, that the Antis, from the region of Peru just north of Cuzco, had a word for the wild potato, presumably in their own tongue, though it might conceivably have been borrowed from Quechua. The word given by LeClerc (1890) is *catzari*, which is defined as ‘papas de la sierra’. This can probably be translated as ‘wild potatoes’, since we have seen that the same type of definition for wild potatoes is often used to-day.

Certain words for the wild potato are mentioned by Mejía in a language known as *Akkaro* or *Kauki*, quoted from an unpublished work by Tello. I have not found any other references to this language and its geographical location was not given. However, as it seems to bear certain affinities to Quechua, and is probably located somewhere in the Andes, the words will be dealt with in Table 5.

A large number of words for the wild potato may also be found in Aymará, the language of the Indians in the altiplano region of south Peru and north Bolivia, chiefly centred round Lake Titicaca. Often these words occur in combination with *choke*, the Aymará word for the potato, but this is not an invariable rule. Certain of the words given in the Quechua list are very probably of Aymará origin, notably *arac*, *kita*, *orkko* and *rukki*, whilst others that have been placed in the Aymará list, such as *kkipa*, may possibly be of Quechua origin. The words *apfaru* and *lillicoya* seem to refer to the truly wild potato when found far from human habitation. A list of the words collected from several sources is given in Table 6.

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[1] This does not coincide by any means with what the Indian thinks about them (see Hawkes, 1944, pp. 101–10).

TABLE 4. *Words used for the wild potato in Quechua*

Word	Source	Meaning and notes	Type	Locality
Alkko papa	J.G.H.	Dog potato	S	Sucre and Potosí, Bolivia
Añas papa	Mejía	'Name of certain types of wild potatoes. Most grow on the punas during the rainy season; there are others that grow in marshes, being suitable for the preparation of food.' *Añas* = a small wolf, hence—= wolf potato	?W	(?) Peru
Aya papa	J.G.H.	Ancestor, ghost potato. So called because it is thought by the Indians to have been cultivated at one time by their ancestors. The name, but not the potato itself, was encountered by me both in Ecuador and Peru[1]	?W	Ecuador, Peru
Arak	J.G.H.	(Also spelt *arac*, *ara'qua*, *araj*, *aracca*, etc.) 'Wild potato' (Mejía). This word also occurs in Aymará districts and may perhaps originate from that language	W	Copacabana, Bolivia; Cuzco, Abancay, Andahuailas, Peru
Atoj	J.G.H.	(Also spelt *atocc*, *ato'q*, etc.) Fox potato. This actually refers to the Peruvian fox, a kind of wolf (*Canis vetulus* sec. Tello). 'Certain kind of wild potato' (Mejía)		Cuzco, Peru
Cachu	Gonç.	'Potato tubers left in the earth at harvest and which are beginning to sprout' (Gonç.). '*Cachu putumun* = to sprout the potatoes forgotten in the earth' (Gonç.). This word seems quite definitely to be applied to 'ground-keepers'	G	(?) Peru
Kkita	J.G.H.	'Wild potato' (Midd., Mejía)	W	Sucre, Bolivia; Andahuailas, Peru
Koyu papa	Gonç.	'Potatoes left behind in the earth at the time of harvest'	G	(?) Peru
Mallcu	J.G.H.	Verbally translated = 'bitter', but may also mean 'wild' or 'mountain'. Applied generally to cultivated potatoes with wild affinities	C	Paucartambo and Chincheros, Peru
Orkko	J.G.H.	Mountain, wild or bitter. Cultivated potatoes with wild affinities	C	Puno, Peru
Ppisco papa	J.G.H.	Bird potato	S	Sucre, Bolivia
Kkapu	Mejía	Wild potato of the same type as *añas papa*	?W	Peru
Rukki	J.G.H.	Wild potato or cultivated potato with wild affinities	?W ?C	Puno and Paucartambo, Peru
Sihua	Mejía	'Escaped potato that in a short time degenerates, becoming like the wild potato'	?G ?W	(?) Peru
Uchika	Mejía	Defined similarly to *añas* and *kkapu*	?W	(?) Peru

The wild potato in Chile has received mention from not a few of the famous travellers who touched on the coast of that country. Probably the first mention is by Febrés in a work published in Lima in 1765 entitled *Diccionario Araucán-Espanol*. In the 1883 edition published at Buenos Aires, which is probably identical with the Lima edition, we find (p. 199):

> '*Malla*: wild potatoes;
> *Mallan*: to gather, cook or eat them.'

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[1] See Hawkes & Howard (1941).

TABLE 5. *Words used for the wild potato in Akkaro or Kauki*

Word	Source	Meaning	Code	Locality
Aipapa	Mejía	'Wild potato.' This is probably a corruption of the Quechua *aya papa* (see Table 4)	W	(?) Andes
Ekako	Mejía	'Escaped potato'	?S	(?) Andes
Muyuko	Mejía	'Escaped potato.' Possibly from the Aymará *mulluncku* (see Table 20)	?S	(?) Andes

TABLE 6. *Words used for the wild potato in Aymará*

Word	Source	Meaning	Code	Locality
Anakachu	Mejía	'Escaped potato'	?S	(?) Peru
Apfaru	J.G.H.	(Also spelt *apharu, aparu, aparoma, apfuruma, aphuruma*, etc.) This is the commonest word for the wild potato in Aymará and is mentioned by many authors (Bertonio, Middendorf and others). It seems to indicate the truly wild as against the weed or semi-cultivated potato	W	Tilcara, north Argentina; Cochabamba, Eucaliptus and Hualata; Bolivia
Ipi amka	Bert.	'Wild, very small potatoes'	?W	(?) Bolivia
Ipi	Bert.	'Small, wild potatoes, growing many from one plant.' Probably derived from the words *ipina, ipipa*=many in number	?W	(?) Bolivia
Japu	Bert.	'Potatoes gathered at the time of sowing' (? ground-keepers)	?G	(?) Bolivia
Kkea	Bert.	'Potatoes that grow when the others are sown, by reason of being left behind in the earth'	G	(?) Bolivia
Kkea	Mejía	'Escaped potato'	G	—
Kkipa	J.G.H.	Plants growing from tubers left in fields from last year's crop; ground-keepers.	G	Eucaliptus, Bolivia
Kkipa choke	J.G.H.	Wild potato	W	La Paz, Bolivia
Lillicoya	Forbes	'Wild potato.' (Also mentioned by Roze (1898, p. 31), quoting an account of Weddel)	?W	Lake Titicaca region, Bolivia
Makunco	J.G.H.	Wild potato. According to Cárdenas the literal translation is 'potato berries'. It was applied to wild *Solanum acaule* growing in fields of cultivated potatoes and may therefore signify a 'degenerated' plant grown from the berries of the cultivated potato in the mind of the Indian who gave me this name. Bertonio (1612) gives for potato berry the word *makuncara*	W	Tiahuanaco, Bolivia

Molina, in his *Geographical, Natural and Civil History of Chile*, published in Bologna in 1787, mentions both cultivated and wild potatoes. After talking about the cultivated tubers he continues: '...but those plants that grow wild, called by the Indians *maglia*, produce only very small roots of a bitterish taste.' In this, Molina uses the Italian spelling, but the pronunciation is identical with the Spanish pronunciation of the word given by Febrés. It is from the Italian spelling, of course, that the name of the wild Chilean potato species *Solanum Maglia* is derived.

The word *malla* (*maglia*) is also mentioned by Claude Gay (1865) and by several other reliable authorities. Wight (1916), however, considers that the word might be confined to the coastal wild potatoes and *poñi* to those that grow in the mountains. The evidence seems more heavily weighted in favour of the view that *poñi* is applied only to the cultivated potato as we have already seen. I have, unfortunately, not been able to obtain any other evidence for or against the view given by Wight that *malla* is restricted to the coastal regions.

Darwin, in his *Voyage of a Naturalist*, mentions that on 7 January 1835 he found wild potatoes on the northern islands of the Choños archipelago. After describing the plants he states that '...they grow as far south, according to Mr Low, as lat. 50°, and are called *Aquinas* by the wild Indians of that part. The Chilotan Indians have a different name for them.'

We have seen above that *malla* was the Araucanian word for wild potatoes and was almost certainly used in the island of Chiloé. South of this island in the region of the Choños archipelago, the Indians are of another race, and it is therefore probable that *aquina* is the word of this Chonoan tribe for the wild potato.

(3) *Other cultivated tubers similar to the potato*

At various times travellers and collectors in the South American Andes have noticed the cultivation of other tuberiferous crops which they have not infrequently confused with the potato itself. We shall therefore devote a brief space to them here in order to try to prevent confusion arising in the future over the status of these plants and their exact identity as distinct from the genuine potato. We do not wish, however, to deal with all the tuber-bearing plants to be found in South America, and shall confine ourselves entirely to those plants that are commonly grown in the same altitudinal belt as the potato and also to the sweet potato which, though grown at lower altitudes and of totally different botanical affinities, nevertheless is apt at times to be confused with the potato owing to a basic confusion between the names of these two plants.

(i) *Ipomoea Batatas*. This is the true sweet potato that was found by the Spanish and Portuguese explorers originally on the shores of the Caribbean Sea, and has at one period or another spread all over the tropical world. Although it is a tropical plant and does not in general coincide in its distribution area with the true potato, some varieties of the latter in the Andes are occasionally named after it, owing to a fancied resemblance in colour, shape or flavour.

The Caribbean word, is, of course, *batata*, and this has been taken into Spanish and Portuguese. For some unknown reason the Latin specific epithet for this plant makes use of the plural form *batatas*. This word has suffered corruption eventually into the English word 'potato', having become transferred by some quirk of fate to the Andean plant, whilst the *Ipomoea* potato has been relegated to second place and distinguished by the qualifying word 'sweet'. Strangely enough, even the original word *batata* in Portuguese now refers to *Solanum tuberosum*, whilst the sweet potato is named 'batata doce'. In Spanish, however, *batata* is equivalent to 'sweet potato', the Spanish word for the ordinary potato being *patata* or *papa*.

One finds certain names for the sweet potato among the Carib Indian tribes from the Guiana regions of the coast of northern South America. Thus another word that seems to be directly related to *batata*, mentioned by Crevaux *et al.* (1882), for the Caribbean tribe known as Cariniaca, is *outata*. According to these same authors the word *napi* is equivalent to potato (and since there are no true potatoes in this region we must assume that they refer to the sweet potato) in the language of the Galibi tribe, whilst Coudreau (1892) records this word also for the Ouayana and Aparaï tongues. A probably related word, *nahi* (=potato) from the Carijona tribe, is given by Crevaux *et al.* The Arrouague word is said by these latter authors to be *aletchi*, whilst the Piapoco word is *cariri*. Coudreau (1892) mentions that the word used for sweet potato in the Émerillon language is *zétic* or *namoua*. These words are in use rather far away from where the true potato could be found, but it was thought to be of interest to include them here.

A very common word in Spanish for sweet potato is *camote*, and though originally belonging to Mexico (?Aztec), it is now almost universally applied throughout South America and is in fact much more common in that region than *batata*.

In Quechua two words are found, *apichu* and *ckumara* (*'kumara*), the latter, accordi to Middendorf, signifying a special white variety.

In Aymará, according to Markham, the sweet potato is known as *tuctuca*, but I ha not been able to verify this; it is possible that the word may be borrowed from the tong of some more lowland tribe, since the Aymarás live at predominantly high elevatio above the upper limit for sweet-potato cultivation. Forbes (1870) gives the word *apich* but we do not know whether this has been borrowed from the Quechua or whether t reverse process has happened.

The Yuracares of east Bolivia know the sweet potato under the name of *seech* according to La Cueva (1893), whilst Leclerc (1890) states that the Antis of the regi north of Cuzco had the word *curiti* or *curhiti* for it.

Uricoechea (1877) states that the Páez word is *unt*, but he does not mention any equiva lent for sweet potato in Chibcha. In Yunga, the language of the Chimu or Muchik peopl of north Peru, Larco Hoyle (1939) gives the words *opex* and *apene* for the sweet potato

(ii) *Ullucus tuberosus*. This is a smooth-skinned tuberiferous plant known under t Spanish name of *papa lisa*. It belongs to the family Basellaceae, allied to the Chenopod and is cultivated at high altitudes though not to the same extent as the potato. T native name, from which the generic name was taken, is *ullucu* (*ulluco*, *olluco*, etc.) an here again the plural form has been taken for the Latin name. The word is known bot in Quechua and Aymará and is mentioned by most vocabularies of these language though it is impossible to tell to which of these it is native. In Colombia, according t my own experience, the *ullucu* is known as *chuhua* (*chugua*) or *ruhua* (*rugua*).

(iii) *Oxalis tuberosa*. The tubers of this plant possess a smooth waxy skin, and are lo with rather numerous, long, deep eyes. As the *ullucu*, it is grown in small quantities high altitudes, and occurs in many colours. The Quechua name is *oka* (*oca*, *occa*, etc.), an this is mentioned by most lexicographers, though rarely distinguished botanically fro the true potato.

According to Forbes (1870) the Aymará word is *apilla*, which also means 'penis' in tha language. This word is also mentioned by Bertonio, who defines it as: 'Potato like th Batata from which they make caui.' According to the *Spanish Academy Historic Dictionary* (1936) the word *cavi* means 'the dried and cooked root of the *oca* of Perú This is confirmed by Forbes (1870), who lists *caui* as 'sweet prepared ocas'. Thus all see agreed that the root itself is *apilla* and the prepared dish *caui* or *cavi*.

In Colombia I found the word *cubio* attached to a tuberous cultivated *Oxalis*, an although the opportunity for examining leaves and flowers of this plant was not availabl it is very probable that it also belonged to the species *O. tuberosa*.

(iv) *Tropaeolum tuberosum*. The plant is cultivated at similar altitudes though t a smaller extent than *Oxalis* and *Ullucus*. Though the tuber is very similar to that of th *Oxalis* in shape, it is of a bitter taste.

The Aymará word is *isañu* (according to Forbes, Cárdenas, etc.), the Quechua nam *añu* (Gonçalez, Middendorf, Mejía) being probably derived from the Aymará. Mejía als gives *añu* = wild potato, but this would seem to be a definite mistake. Another wor given by Mejía for this tuber is *mashhua* (also spelt *mishwa*), though this word has no been seen in other dictionaries; neither has the word *allausu* which he also mentions. It i possible that these two words may not be Quechua, since the *sh* sound in *mashhua* is no to be found in that language.[1] Middendorf, however, lists the word *maca*, which h defines simply as an 'edible root similar to the potato'. It is possible that this word ma be a corruption of *mashhua* or vice versa.

It is worthy of note that MacMillan and Erlanson, who travelled in South Americ collecting potatoes for the U.S. Bureau of Plant Industry, obtained a sample of *Tro paeolum tuberosum* at Tarma under the name of *Massua*. Tarma is situated in Per department Junín, where the Chinchaysuyo dialect was once spoken; it is possible therefore that this word belongs to Chinchaysuyo and is not of widespread occurrence.

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[1] Some authorities, such as Tello, consider the *sh* sound to be normal in Quechua, and Tello himse spells this latter word *Keshwa*.

The information that we have presented above on the native names of these tuber-bearing food crops that have sometimes been confused with the potato gives us no information on the various names given to this latter plant. The words for *Ullucus tuberosus*, *Oxalis tuberosa* and *Tropaeolum tuberosum* are quite distinct, and one must evidently look elsewhere for clues on the origin of such words as *papa*, *amka*, *choke* and *ajsu*.

PART III. THE VARIETAL NAMES OF POTATOES IN QUECHUA AND AYMARÁ

(1) *Introduction*

Having reviewed the names applied to the potato in the various Andean languages of the regions where it is grown, we are now in a position to consider in more detail the names of the different potato *varieties*.

As we mentioned above (p. 205), the names dealt with in the present section are confined to the two languages Quechua and Aymará, since Spanish words are easily translatable with the aid of a good dictionary. Also, to avoid confusion I shall confine myself to names of potatoes collected by myself and my colleagues or that I have later been able to study in collections sent to me from South America. Although there is probably an interesting study awaiting elucidation of the Araucanian potato variety names, I have no first-hand experience of these and have therefore thought it better to leave this to someone who has actually travelled and collected in Chile.

The degree of accuracy in naming a potato variety varies enormously amongst the American Indians of the Andes, and whilst it would be true to say that in certain districts the accuracy almost equals that of the countries of Europe and North America, in others it certainly falls far short of this standard. In general, the names are more accurately known in the more predominantly Indian districts where European influence is the least felt. In these districts, too, the largest number of varieties is grown: it is surprising, but apparently true, that the standards of skill in naming the varieties are far higher where a large number of varieties occur.

Often one variety may receive different names if it spreads into different districts and when named by more than one person; conversely, one name may apply to several different varieties in the same or, more generally, in different districts owing perhaps to some superficial similarity between them.

It might, perhaps, be as well at this stage to define what we mean by the term 'variety', since this word may have several different connotations. As Bukasov (1933) has pointed out, the word 'variety' when applied to South American potatoes is not synonymous with that used in the rest of the world for the commercial domestic potatoes. In the latter case it refers to a clone of asexually reproduced individuals all originating from one plant in the first instance by the simple method of tuber propagation. In the former, however, it applies to a set of individuals possibly produced from seed, though often by tubers only and having more or less superficial similarity, especially in tuber characters. It is therefore rather wider than the domestic potato variety, since it does not presuppose strict genetic homogeneity. It also does not correspond to the botanical sense of the term 'variety', which may comprise similar or different native varieties grouped together because of taxonomic relationships. The botanical variety is therefore even wider in its connotations. In the present work we shall use the term 'variety' as applied by the Indians, meaning plants with similar tuber characteristics.

Almost without exception the South American cultivated potatoes are named according to their tuber characteristics, the haulm and flower being of no account in identification.[1]

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[1] According to Cárdenas (personal communication), however, the Bolivian Indians can distinguish the *Runa* and *Imilla* varieties by the flower colour and *Luki* by the foliage. The *names*, nevertheless, are applied to the tubers.

When seeing a plant growing in the field and wishing to know the variety, very fe Indians are able, in my experience, to name it without exposing some of the tubers. O the other hand, all varieties can be named by them when inspecting the tubers in a sto or clamp, without any recourse to the stem, leaf and flower characters. A possibl exception to this rule will be dealt with below (see Table 12).

In accordance with this habit of basing the varietal names on the tuber character alone, all the classifications made by Peruvian and Bolivian botanists and agronomist such as that of Cevallos Tovar (1914), Herrera (1931), Vargas (1936) and Soukup (1939 are based on tuber characters. It is therefore to be expected that their systems c classification will be 'artificial', that is, they will seldom, if ever, give any indications c the true phylogenetic relationships of the potatoes under consideration, since the tube characters are the most liable to be altered by selection for colour, yield, shape, etc even though in a quite unscientific way, by the Indian peasantry. Leaf and flowe characters, on the other hand, are less likely to be influenced by selection or by the force of the environment; the flowers especially, even more than the leaves, are of paramoun importance in assessing the true relationships of the different varieties.

With few exceptions potatoes receive two names by the Indians, generally in one o other of the two most widely spread native languages, Quechua and Aymará, or sometimes in Spanish. One word is generally a noun, the other a qualifying adjective Occasionally one finds two descriptive adjectives, though one of these may be used in th sense of a noun. Rarely the name consists of one noun with two adjectives. It is fairl common in districts where the indigenous language is spoken side by side with Spanis to find mixed names, one word being in Aymará or Quechua and the other in Spanish occasionally (in Bolivia and South Peru) one may find a name composed of one Aymar and one Quechua word. With these two mountain Indian languages the adjective i always placed before the noun, as in English, whereas in Spanish the reverse is usuall the case. In mixed names the adjective generally tends to be Spanish and the nou Aymará or Quechua, and in these cases the adjective also follows the noun. Commonl the adjective is one describing colour whilst the noun may not necessarily be descriptive but may be applied to tubers of a certain shape or with certain physiological properties such as taste, succulence, time of maturity, etc.

(2) *The distribution of varietal names*

It may be of interest, before inquiring into the meaning of the names applied to th South American potato varieties, to see how the distribution of native names among th three languages varies with the geographical position from where the varieties wer collected.

Table 7 shows the number of varieties with names in Spanish, Quechua, Mixed Spanis and Quechua, Aymará, Mixed Spanish and Aymará, and Mixed Quechua and Aymar respectively for each department where potatoes were collected by myself and m colleagues.

The words have been grouped geographically according to the main departmenta divisions of the countries through which the expedition passed, proceeding from south t north. The departmental grouping has not been practicable in Ecuador, which is a muc smaller country and is divided into provinces. Here we have dealt with two groups only namely, south Ecuador (provinces Cañar and Azuay) and north Ecuador (province Chimborazo, Tungurahua, León, Pichincha, Imbabura and Carchi). Colombia, also, ma very conveniently be divided into two parts for our present purposes—the sout (departments Nariño, Cauca and Valle del Cauca) which is geographically and floristicall closely connected with north Ecuador, and the central region (departments Cundinamarc and Boyacá), which is considerably isolated in its potato varieties from the south.

The table has been compiled from the native names of 1039 varieties collected b myself and my colleagues in South America, and care has been taken to render it a

Table 7. *Frequency of potato names in Spanish, Quechua and Aymará in various parts of the South American Andes*

Country	Department	Total no. of names	Spanish		Quechua		Spanish-Quechua		Aymará		Spanish-Aymará		Quechua-Aymará		?	
			No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
N. Argentina	Jujuy (province)	15	8	53	3	20	2	13	—	—	—	—	—	—	2	13
Bolivia	Tarija	30	16	53	7	23	5	17	1	3	—	—	—	—	1	3
	Potosí	15	—	—	4	27	2	13	1	7	4	27	—	—	4	27
	Chuquisaca	22	—	—	8	36	—	—	2	9	3	14	5	23	4	18
	Cochabamba	155	22	14	23	15	12	8	30	19	15	10	17	11	36	23
	Oruro	36	1	3	—	—	—	—	25	69	4	11	—	—	6	17
	La Paz	121	6	5	1	1	2	2	70	58	9	7	1	1	32	26
Peru	Puno	98	8	8	13	13	2	2	30	31	6	6	13	13	26	27
	Cuzco	173	14	8	80	46	11	6	7	4	2	1	17	10	42	24
	Apuímac	41	5	12	25	61	2	5	—	—	—	—	1	2	8	20
	Ayacucho	32	5	16	18	56	3	9	—	—	—	—	—	—	6	19
	Junín	49	28	57	8	16	5	10	1	2	—	—	—	—	7	14
Ecuador	[South]	29	15	51	4	14	6	21	—	—	—	—	—	—	4	14
	[North]	83	53	64	15	18	3	4	—	—	—	—	—	—	12	14
Colombia	[South]	45	24	53	4	9	13	29	—	—	—	—	—	—	4	9
	[Central]	95	84	88	1	1	1	1	—	—	—	—	—	—	9	10
	Total	1039	289	27	214	22	69	7	167	16	43	4	54	5	203	19

accurate as possible. Certain names were found to occur more than once but were counte for every occurrence, since it was felt that this would give a more accurate indication the prevalence of each language in the particular area group analysed. If the meaning one word of the pair that together comprise the name of the potato variety was unknow or doubtful the name was counted in the last column of the table.

The percentage of words in this last column may at first sight seem rather large. This i due to the fact that many potato names, especially from the Aymará-speaking district could not be found in any dictionary, and whilst it was possible to hazard a guess as t their language it was felt better not to place them unless their affinities were known wit certainty. The lack of good Aymará dictionaries probably contributes to the hig percentage of untranslatable words for Bolivia and Peru, which otherwise might be adde to the Aymará list. In Ecuador and Colombia, however, the doubtful words are certainl not Aymará, since that tongue was never spoken there. They have probably been take from languages other than Spanish, Quechua or Aymará. All the untranslatable words those whose meaning is not known with certainty will be found listed in an Appendi to this paper, together with a note on their provenance. It is very much hoped tha future workers on this subject may be able to elucidate their meaning.

One final note before we continue to examine the table in more detail. The word *pap* which is often found in varietal combinations has been treated for the purposes of th table as linguistically 'neutral', since although primarily a Quechua word it has becom so universal in Spanish that one cannot consider it now as exclusively Quechua. An combination with *papa*, therefore, has been placed in the column appropriate to th language of the second word of that combination.

Let us now go on to examine Table 7 in detail. If we review the percentage of Spanis names in the different districts we shall see a high percentage at either end of our range declining to zero towards the centre. Roughly speaking, the percentage of Spanish word increases the farther one progresses from the centre of the Inca empire at Cuzco, whils outside the former confines of that empire in central Colombia the percentage of Spanis words is very high indeed (88 %). In the Bolivian departments of Potosí and Chuquisac Spanish potato names were not found, and even Spanish-Quechua and Spanish-Aymar combinations were rather low.

From Argentina northwards into Bolivia the percentage of Quechua words, whic starts at 20 %, increases to about the region of Chuquisaca and then decreases to abou zero in departments Oruro and La Paz. The opposite is roughly the case with Aymará which shows a maximum in the Oruro and La Paz region. The accompanying ma (Map 2, p. 229) will serve to make this point clear. Spanish-Aymará mixtures are absen in north Argentina and south Bolivia, high in the centre and slightly decreasing toward the north in the department of La Paz. Spanish-Quechua combinations are found chiefl in Argentina and south and central Bolivia, decreasing very much in the districts wher Aymará names predominate.

This distribution of the names in Bolivia and Argentina corresponds moderately wel with the distribution of the native populations. Thus in the region of La Paz and Lak Titicaca only Aymará-speaking Indians are to be found. Southwards from departmen Cochabamba the native dialect is Quechua, owing to the fact that large colonies (mitimaes of Quechua-speaking Indians were 'transplanted' from Peru into Bolivia during the Inc colonial period. But even in the departments of central and southern Bolivia one ca see that many Aymará words exist either in pure Aymará names or in ones mixed wit Quechua or Spanish; several Aymará words have indeed been taken into the Quechu language of these regions, and this is especially noticeable with potato names as we sha see again later.[1]

[1] According to Dr M. Cárdenas (personal communication), Aymará words still predominate for a geographical names, even in Quechua-speaking districts such as departments Cochabamba an Chuquisaca.

In the north Argentine province of Jujuy the number of potato varieties is diminished, the peasant population is not so exclusively pure Indian as it is farther north, and hence more Spanish words have been introduced. Certain Quechua and Spanish-Quechua combinations do, however, occur here.

The Cuzco region of south Peru, which was the centre of the Quechua-speaking Inca civilization, is, as one would expect, predominantly Quechua in tongue at the present day, only a small percentage of the potato names being Spanish or Spanish-Quechua.

Of very particular interest here is the occurrence of 10 % Quechua-Aymará, 4 % pure Aymará and 1 % Spanish-Aymará names in this region. Even in department Apurímac, farther away still from the Aymará districts, one Quechua-Aymará word was encountered. Yet Aymará is not spoken in these regions at the present day; nor was it during the Inca colonial period except possibly by Aymará Indians visiting the capital, who certainly did not cultivate any plants there nor introduce their own language.

There are at least three hypotheses to account for this phenomenon of Aymará words occurring in Quechua districts. In the first place these regions may have been inhabited by Aymará Indians before the advent of the Incas who, when they arrived, took over the plants and plant names already indigenous to the district. The second is that the Aymarás, who are often supposed to pre-date the Incas, were the original domesticators of the potato, and that the Incas took many Aymará names together with the potatoes back to their own districts when they had conquered the Aymará tribes from the region of Lake Titicaca. The third is that during the Inca and possibly Spanish colonial periods there was frequent interchange of the food plants from different parts of the Andes and that many potatoes from Aymará districts were taken to Quechua districts. The reverse process, however, seems to have been much rarer, though one would expect it to be more common, since the Aymarás were a comparatively small conquered tribe surrounded by Quechua districts and in an empire whose policy was the suppression of native tongues and their superimposition by the Quechuan *lingua franca*. Probably archaeological or ethnographical studies might help in deciding which of the three hypotheses outlined above might be most probable.

To return to our discussion of the table; the figures given for department Puno in south Peru refer to the whole department, which includes both the southern Aymará-speaking districts and the northern Quechua-speaking areas bordering on Cuzco. There is here a high percentage of Aymará names, together with a few Quechua, Spanish and mixed names in various combinations.

In department Apurímac, Quechua names predominate, the Spanish and Spanish-Quechua combinations being rather low. As we mentioned above, one Aymará word was encountered in this department.

The position for department Ayacucho is fairly similar, though here the Spanish words begin to creep in again, whilst in the more commercially developed, less Indian district of Huancayo (department Junín), Spanish names predominate. Even here, one Aymará word was found.

No collections were made in Peru north of department Junín, but probably the Spanish element would be rather high. It would be of especial interest to collect varieties from the northern departments of Peru to see whether any words from the Yungan or Muchik tongue have been drawn into use in naming the local varieties. However, up to now no collections have been made from those regions in a systematic way.

In Ecuador, Bukasov (1930) quotes Popenoe as stating that there are no native potato names for that country, nor for Colombia and central Peru. We have seen in the case of department Junín, which undoubtedly lies in central Peru, that there are only 57 % of Spanish names, the rest being in Quechua or Spanish-Quechua. Indian names, also, most certainly occur in Ecuador and in south Colombia, since the proportion of Spanish names never rises higher than 64 %. Similarly with central Colombia there are a few Quechua names to be found, though here by far the largest proportion is Spanish (88%).

Ecuador and south Colombia had only been brought under Inca domination in the latter part of the fifteenth century, some few decades before the Spanish conquest, and hence although the Quechua language had been imposed upon the indigenous tribes it probably did not completely replace all the words of the original Indian languages. Certain names occur in Ecuador and south Colombia that certainly are not Spanish or Quechua, though in most cases I have not yet been able to trace their etymology (see Appendix, p. 245). In one case, however, it seems fairly certain that a word from another tongue is in current use. The word 'Chimbalo', or 'Chimbalan', applied to potatoes grown from true seed, a custom unique for the whole of South American indigenous potato culture, seems, so far as I have been able to ascertain (Jíjon y Caamaño, 1919) to belong to the Barbacoa group of languages (though not, apparently, to the tongues Colorado and Cayapa). It is possible that, since the word seems to indicate in its present meaning a fruit or a berry of the potato plant, the original Barbacoa word may also mean 'fruit' or 'berry'. Unfortunately, no vocabulary of Barbacoa (if one indeed exists) has been available to enable me to verify this supposition.

Colombia was never conquered by the Incas, except for the southern regions with which we have already dealt above; hence in the central departments Quechua words are almost, but not quite, absent. One Quechua and one Spanish-Quechua name were encountered. This central area was inhabited by the Chibcha Indians; but although there were quite a few Chibcha varietal names in the early days of the conquest (see above p. 213), it is doubtful whether many exist at the present day, though the philologist might be able to decipher some from the list of words given in the Appendix to this paper. It is not impossible, however, that a persistent search in the more inaccessible regions of central Colombia might bring to light certain Chibcha words lingering only in the names of potato varieties as they do in geographical place-names.

Such a process has taken place in other areas, such as in north Ecuador with the Barbacoa word 'Chimbalan', and in parts of Peru and Bolivia with a number of Aymará words, the original meanings having been entirely lost in those regions where the words are now found.

(3) *Lists of the Aymará and Quechua words used in potato names*

In our final section we shall now consider the different varietal names and their meanings, dealing with the words separately, though in the names there are generally two, a noun and a qualifying adjective.

It should be reaffirmed that the lists given below do not claim to be a complete vocabulary, since only the words are given which occurred in the names of potatoes which I collected and which it was possible to translate. The authorities for the translations are given in an abbreviated form after each word; the full name is given at the end of this section, the exact reference to the publication being found in the bibliography. In the cases of very common words only the best-known authority is given.

In addition to the words and their meanings a few examples of the potato names in which each word occurs will be given together with the translation. It has not been possible to include all the combinations, especially in the case of the colour variations of certain types of potatoes which may have up to twenty or thirty different colour forms. In these cases only the commoner ones are given.

It has also been thought of use to include a very brief note of the country and region in which each name occurs, and this will be found in the third column of the following word lists.

The Aymará and Quechua words are dealt with in separate lists; if there is doubt as to the original language for a word which occurs in both, a footnote is included to that effect.

The words have been arranged into categories, as follows, the nouns being dealt with first:

I. *Nouns* (Tables 8–16):
  (*a*) Men (including women, children and other relatives).
  (*b*) Animals.
  (*c*) Parts of the body.
  (*d*) Clothes.
  (*e*) Plants.
  (*f*) Foodstuffs, etc. (excluding certain edible plants to be found in the previous section).
  (*g*) Tools, implements.
  (*h*) Natural objects and phenomena.
  (*i*) Miscellaneous.

II. *Adjectives* (Tables 17–20):
  (*a*) Colour.
  (*b*) Shape, size.
  (*c*) Surface, texture, taste.
  (*d*) Miscellaneous.

III. *Classes of potatoes* (Table 21):

This group includes special very well-known types of potatoes with names of unknown meaning.

IV. *General potato names* (Table 22):

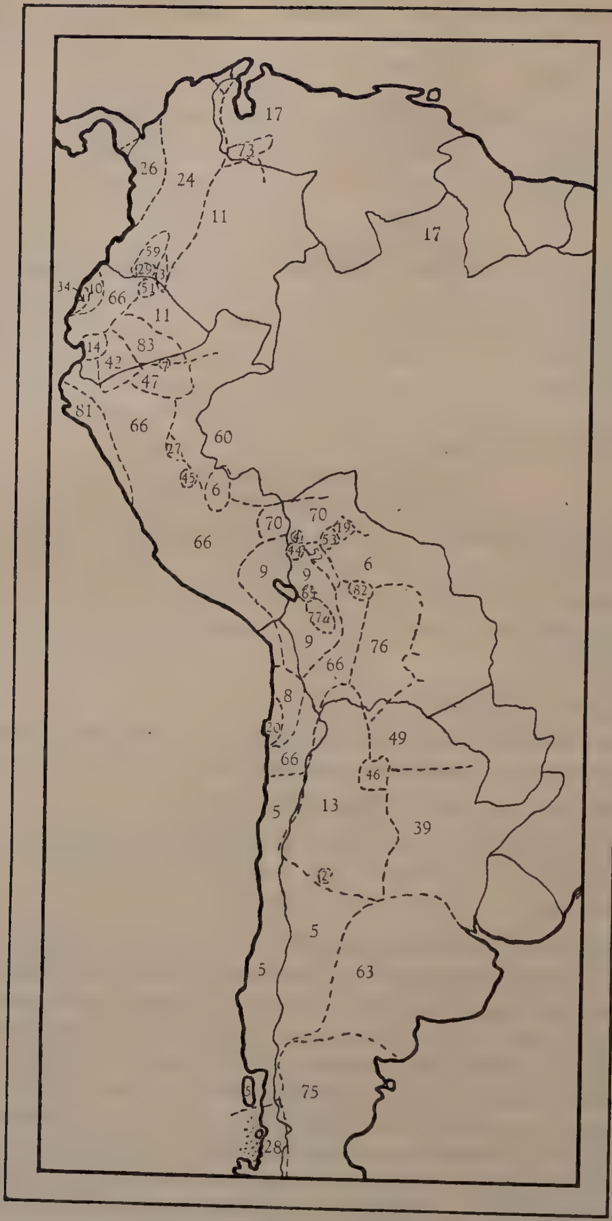
Here have been placed all words applied to potatoes irrespective of and in addition to their own special varietal names.

V. *Words connected with potato cultivation* (Table 23):

This group has been compiled from the dictionaries and vocabularies of Aymará and Quechua available to the author, and includes all the words or phrases that are given in connexion with potato cultivation.

The names included in group III (Table 21) call for more explanation at this point. This list includes names that are either not mentioned in the dictionaries, or, where they occur, have no meaning, except that they apply to certain sorts of potatoes; even in their indigenous language, apparently, they are just names without any meaning renderable in terms of other words. Such, for example, is the Aymará word *luki*, which refers to frost-resistant bitter potatoes, or *chapiña*, which refers to those types from which a dye is extracted. It is quite possible that such names may have been borrowed from some earlier language of a conquered Indian tribe; the word is retained, but all knowledge of its original meaning has been lost with the disappearance of the language whence it was derived, except for those few words incorporated into the tongue of the conquerors.

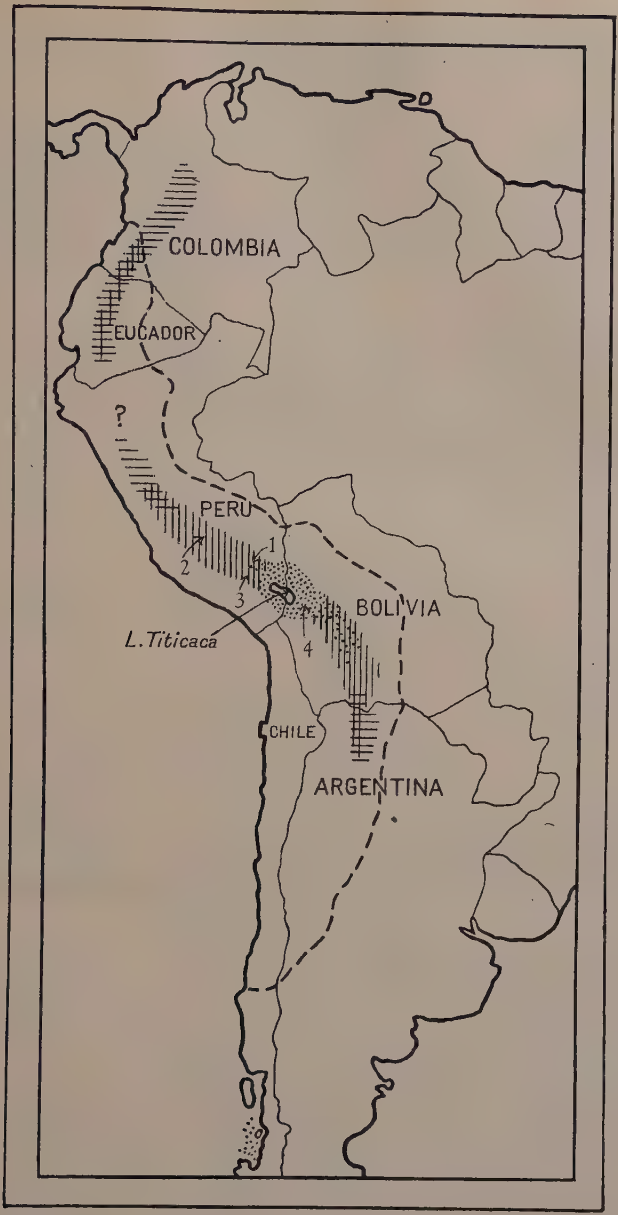
Thus, for example, in Bolivia one of the commonest potato names is *imilla*, an Aymará word meaning 'girl'. Both this word *imilla* and the Quechua word *runa* (=man) are applied to certain classes of potatoes and should perhaps be placed in group III; since their translation was known, however, it was thought better to list them with the other translatable words. The Aymará word, *imilla*, is applied to a class of isodiametric or sometimes rather axially compressed potatoes with rather deep round eyes. The word has been incorporated into the Quechua-speaking districts of central Bolivia, though here its meaning is not realized, and it is considered only as a name with no other meaning other than referring to a certain type of potato. It seems very possible that this process may have occurred very frequently and may account for the untranslatability of many of the names that we have placed in group III (Table 21).



Map 1. Linguistic stocks of the Andean Indians (adapted from Chamberlain, 1913).

Key to stocks shown on the Map.

2. Allentiacan
3. Andaquian
4. Apolistan
5. Araucanian
6. Arawakan
7. Ardan
8. Atacameñan
9. Aymaran
10. Barbacoan
11. Betoyan
13. Calchaquian
14. Cañarian
17. Cariban
19. Cayubaban
20. Changoan
24. Chibchan
26. Chocoan
27. Cholonan
28. Chonoan
29. Coconucan
30. Esmeraldan
31. Guaycuruan
42. Jivaran
44. Lecan
45. Lorenzan
46. Lulean
47. Mainan
49. Matacan
51. Mocoan
52. Mosatenan
53. Moviman
59. Paniquitan
60. Panoan
63. Puelchean
65. Puquinan
66. Quechuan
70. Tacanan
73. Timotean
75. Tsonekan
76. Tupian
77*a*. Uran
81. Yuncan
82. Yurucarean
83. Zaparan



Map 2. Potato names in the South American Andes in the languages Spanish, Quechua and Aymará

Spanish ▤
Quechua ▥
Aymará ░

------ Approximate boundary of the Inca Empire (Tahuantinsuyo).
The four main regions of the Empire were:

1. Anti-suyo. 2. Chinchay-suyo. 3. Cunti-suyo. 4. Collay-suyo.

(Regions 2 and 4 stretch some distance northwards and southwards respectively from the points shown on the map.)

Further study of the group of related languages in and around the Andes might help to elucidate many of these etymological problems that I can do no more than present.

In such an ancient cultivated plant as the potato, whose beginnings are so closely interwoven with those of the Andean Indian cultures, it is to be expected that the complexities that exist may be unravelled only by a close combination of ethnological, etymological and botanical studies. The present work has to some extent reviewed the field, pointed out certain problems, and stressed in many places the need for further work by the philologist, both on the languages as they exist at the present day and on the old manuscripts that were compiled by the earliest European visitors to the Andes and which dealt with tongues or dialects that have now often become extinct.

Botanical and genetical studies on the cultivated potato have already furnished some indications as to the centre of origin of this plant, and we are now fairly certain in our surmise that it was first brought into cultivation in the region of Cuzco and the Lake Titicaca basin; yet by what tribes or in what manner is not known. So far, also, the study of the plant from the linguistic point of view has furnished little evidence either to support or refute the botanical hypotheses that we have just mentioned. Although there is a great deal of information that we perhaps shall never be able to obtain, nevertheless I am convinced that a great deal of fruitful research might be conducted along some of the lines indicated in the present paper. By so doing we shall without doubt be able to solve certain problems of the evolutionary history and phylogenetic relationships of the potato on the one hand, whilst on the other further contributions to our knowledge of the early Indian cultures may be confidently expected.

Key to authority abbreviations mentioned in Tables 8–23

Asc.	Sr L. Ascásabi, Quito, Ecuador. (Personal notes kindly supplied to the author.)
Bert.	Bertonio, L., *Vocabulario de la Lengua Aymará.*
Cárd.	Dr M. Cárdenas, University of Cochabamba, Bolivia. (Personal and written notes kindly supplied to the author.)
Cat.	(Anonymous), *Catálogo de las Voces Usuales de Aimará, Castellano y Quechua.*
Cev.	In Ballivián, M. V. and Cevallos Tovar, W., *Noticia Histórica y Clasificación de la Papa de Bolívia.*
Forbes	Forbes, D., *The Aymará Indians of Bolivia and Peru.*
Garc.	García, J. A., *Gramática Aymará.*
Gonç.	Gonçalez Holguín, D., *Vocabulario de la Lengua General de todo el Perú Llamada Lengua Qquichua, o del Inca.*
Herr.	Herrera, F. L., *Catálogo Alfabético de los nombres vulgares y científicos de plantas que existen en el Perú.*
Mark.	Markham, C., *General Language of the Incas of Peru.*
Mej.	Mejía Xesspe, M. T., *Kausay. Alimentación de los Indios.*
Midd.	Middendorf, E. W., *Wörterbuch des Runa Simi oder der Keshua-Sprache.*
Midd.	Middendorf, E. W., *Die Aimará-Sprache.*
Souk.	Soukup, V., *La clasificación de las papas del departamento de Puno.*
Tasc.	Tascón, L., *Quechuismos usados en Colombia.*
Varg.	Dr C. Vargas, Cuzco University, Peru. (Personal and written notes kindly supplied to the author.)
Vocab.	(Anonymous), *Vocabulario políglota Incaico Keshua del Cuzco.*
Yabar	Sr L. A. Yabar, Paucartambo, Peru. (Written notes kindly supplied to the author.)

I. NOUNS

Table 8. (*a*) *Men*

Word	Examples	Locality
	Aymará	
Chacha: man (Cat.), man in the sense of male (Cárd.)	*Chachaza*: big man	Puno, Peru
Llockalla: boy (Cev.), boy or unmarried man (Cárd.)	*Ll. blanca*: white boy	Cochabamba, Bolivia
	Puca ll.: red boy	Cochabamba, Bolivia
	Papa ll.: boy potato	Tarija, Bolivia
Imilla: girl (Bert.), girl or unmarried woman (Cárd.)	*Chiar i.*: black girl	N. Bolivia
	Jankko i.: white girl	N. Bolivia
	Yana i.: black girl	Puno, Peru
	Yurac i.: white girl	Cochabamba, Sucre, Bolivia
	Huila i.: red girl	Puno, Peru; N. Bolivia
	Puca i.: red girl	N. and C. Bolivia
	Alkka i.: variegated girl	N. and C. Bolivia
	Chupica i.: cherry coloured girl	Puno, Peru
	Chumpi i: brown girl	Achacachi, N. Bolivia
	Kkellu i.: yellow girl	Sucre, Bolivia
	[Many other variations and combinations occur with Spanish and Quechua adjectives, too numerous to detail here]	[The word is confined to Bolivia and department Puno in S. Peru]
	Quechua	
Runa: man (Midd.), in the sense of mankind (Cárd.)	*R.*: man	Cochabamba, C. and S. Bolivia
	Azul r.: blue man	Cochabamba, Bolivia
	[Many other combinations occur, but almost always with Spanish adjectives]	[Spreads from N. Argentina to C. Bolivia]
Tata: old man (Cárd.), Aymará Indian (Cárd.)	*T. runa*: old man or Aymará man	Tarija, Bolivia
Tatacu: old man (Yabar), Indian (Cárd.)	*Puca t.*: red old man	Paucartambo, Peru
Makktta: Indian (Yabar), cholo (Yabar)	*Yana m.*: black Indian	Paucartambo, Peru
	Yana sonkko m.: black heart of Indian	Paucartambo, Peru
Huirackocha: gentleman (Cárd., Yabar)	*Lima h.*: gentleman of Lima	Paucartambo, Peru
Inca: Inca (Midd.)	*I. papa*: Inca potato	Copacabana, Bolivia
Huarmi: woman (Midd.) or wife (Cárd.)	*Alkka h.*: variegated woman	Paucartambo, Peru
	Kkekkrana h.: frivolous woman	Paucartambo, Peru
Mama: mother (Midd.) or old woman (Cárd.)	*Puca m.*: red mother	Paucartambo, Peru
Ppasña: woman or unmarried girl (Midd.)	*Pp.*: woman	Abancay, Peru
	Huira pp.: fat woman	Ayacucho, Peru
	Pp. papa: woman potato	Andahuailas and Abancay, Peru
Ppasñacha: little Indian girl (Yabar)	*Pp.*: little Indian girl	Paucartambo, Peru
Huahua: baby (Midd.)	*Ttanta h.*: bread baby*	Cochabamba, Bolivia
Cachan: daughter-in-law (Cárd.)	*C. huacachi*: [potato] that makes the daughter-in-law cry†	Cochabamba, Bolivia
Aya: corpse, ghost, ancestor (Midd., Cárd., etc.)	*A. papa*: ghost or ancestor potato‡	Cuzco, Peru; Riobamba, Ecuador

* So called from its fancied resemblance to the 'bread baby' made on All Saints' Day, 1 November. The origin of the custom appears to be unknown. See also Overbeck, A. o'R. (1934), where this custom is described in detail.

† This potato, according to Dr Cárdenas, has deep eyes and is hence difficult to peel. The work is done by the daughter-in-law who lives in the household of her husband's parents.

‡ The name is applied to certain wild potatoes that are supposed by the Indians to have been once cultivated by their ancestors.

TABLE 9. (*b*) *Animals*

Word	Examples	Locality
	Aymará	
*Ckusillu**: monkey, devil (Midd., Cárd.)	*C. negro*: black monkey or devil	Cochabamba, Bolivia
*Huicuña**: vicuña (Midd.)	*H. imilla*: vicuña coloured girl	Cochabamba, Bolivia
*Huallata**: *Bernicla melanoptera*, an aquatic water bird with red feet, white breast and black wings (Midd., Cárd., Yabar)	*H. chinchi*: young *B. melanoptera*	Paucartambo, Peru
*Huaca**: cow (corrupted from the Spanish *vaca* = cow)	*H. ñuñu*: cow's udder	Puno, Peru
	[Many other examples from Peru and Bolivia]	
	Quechua	
*Llama**: llama (Midd., etc.)	*Ll. cuncan*: llama's neck	Abancay, Peru
*Alpaca**: alpaca (Midd., etc.)	*A. chuchulli*: alpaca's feet	Cochabamba, Bolivia
	A. naza: alpaca's nose	Puno, Peru
Puma: puma, the American lion (Midd., etc.)	*P. maqui*: puma's paw	Puno, Peru
	P. moro: purple puma	Puno, Peru
Alkko: dog (Midd., Gonç.)	*A. papa*: dog potato†	Potosí and Sucre, Bolivia
Atoj: fox (Midd.), *Canis vetulus*	*A. papa*: fox potato†	Jujuy, N. Argentina; Cuzco, Peru
Kohui: guinea-pig (Cárd.) [also spelt *Ckoe* (Yabar)]	*K. compadre*: guinea-pig's friend	Cuzco, Peru
	Muru k. sullu: spotted guinea-pig foetus	Paucartambo, Peru
	K. amaro: guinea-pig poison	Paucartambo, Peru
Cuchi: pig (Midd., Cárd., Gonç.) [also spelt *Cjuchi*, *Kuchi*, etc.]	*C. aca*: pig dung	Cochabamba, Bolivia; S. and C. Peru
Condor: condor (Midd., etc.)	*C. huallko*: condor's collar	Puno, Peru
	C. imilla: condor girl	Cochabamba, Bolivia
	C.: condor	Saquisilí, Ecuador
Anca: eagle (Midd., Varg., Gonç.)	*Kkellu a.*: yellow eagle	Chincheros, Peru
Huamán: falcon (Midd., Gonç., etc.)	*H. uma*: falcon's head	Paucartambo, Abancay and Andahuailas, Peru
	H.: falcon	Huancavelica, Peru
	H. chupa: falcon's tail	Puno, Peru
Huashua: heron, stork (Midd.)	*H. kallu*: stork's tongue	Abancay and Quishuara, Peru
Kkalla: wild parrot, green and red (Midd.)	*K. tinya*: parrot tambourine (?)	Abancay, Peru
Llutu (or *Yutu*): partridge (Mej., Gonç., Yabar)	*Ll.*: partridge	Cañar, Ecuador
	Ll. runtu: partridge egg	Paucartambo, Peru
Lequechu: small bird found on the puna (Varg.)	*L.*: small bird found on the puna	Tampu machay, Peru
Allkamari: species of bird (Midd.), *Polyborus brasiliensis* (Cárd.)	*A.*: *Polyborus brasiliensis*	Sucre, Bolivia
Ckellhua: gull (Midd., Yabar)	*Ck. ckocha*: gull lake	Paucartambo, Peru
Chinchi: nestling (Yabar)	*Huallata ch.*: nestling Huallata	Paucartambo, Peru
Runtu: egg (Midd.)	*R.*: egg	S. and C. Peru
	[Many examples coupled with different colour adjectives]	
*Katari** [or *Catari*]: snake (Cárd., Midd., Mark.)	*K. papa*: snake potato	Cochabamba, Bolivia

* These words are used in both languages.
† Names given to weed potatoes, never to truly wild forms.

TABLE 10. (*c*) *Parts of the body*

Word	Examples	Locality
	Aymará	
Naza: snout, muzzle, nose (Cat., Mark.)	*Alpaca n.*: alpaca's snout	Puno, Peru
Lajra: tongue (Bert., Mark.)	*Huaca l.*: Cow's tongue	Puno and Paucartambo, Peru
	Azul l.: blue tongue	Puno, Peru
Chuchulli: animal's foot (Cárd.)	*Alpaca ch.*: alpaca's foot	Cochabamba, Bolivia
	Quechua	
Maqui: hand, paw, forearm (Midd.)	*Puma m.*: puma's paw	Puno, Peru
	Yana puma m.: black puma's paw	Paucartambo, Peru
	Muru puma m.: spotted puma's paw	Paucartambo, Peru
Uma: head (Midd., Yabar)	*Huaman u.*: falcon's head	Abancay and Andahuailas, Peru
	Puca huaman u.: red falcon's head	Paucartambo, Peru
	Huaman u. negra: black falcon's head	Paucartambo, Peru
Ñahui: eye (Midd.)	*Puca ñ.*: red eyes	Cochabamba, Bolivia; Quisahuará, Peru; Saquisilí, Ecuador
	Azul ñ.: blue eyes	Cochabamba, Bolivia
Senka: nose (Midd.)	*Huaca s.*: cow's nose	Ayacucho, Peru
Kallu: tongue (Yabar, Gonç., Cárd.)	*Huaca k.*: cow's tongue	Paucartambo, Peru
	Huashua k.: stork's tongue	Abancay, Peru
Huajra: horn, of cows, etc. (Midd.)	*Huaca h.*: cow's horn	Puno, Peru
Huallko: collar, throat (Midd., Gonç.)	*Condor h.*: condor's throat	Puno, Peru
Sonko: heart (Midd., Yabar)	*Puca s.*: red heart	Cuzco, Peru
	Yana s. makktta: black heart of Indian	Paucartambo, Peru
	Pfuña s.: heart of fern	Paucartambo, Peru
Chupa: tail (Midd.)	*Cuchi ch. morada*: purple pig's tail	Potosí, Bolivia
	Huaman ch.: falcon's tail	Puno, Peru
Chilena: marrow of bones (Midd.)	*Huaca ch.*: cow's marrow	Paucartambo, Peru
Pfuru: feather (Midd.)	*Chejchi pf.*: grey feather	Paucartambo, Peru
Ñuñu: udder (Midd., Garç., Cárd.)	*Huaca ñ.*: cow's udder	Puno, Peru
Cunca: neck (Cárd.)	*Llama c.*: llama's neck	Abancay, Peru
*Sullo**: foetus (Midd., Cárd., etc.)	*Moro kohui s.*: purple guinea-pig foetus	Paucartambo, Peru
	Azul kohui s.: blue guinea-pig foetus	Paucartambo, Peru
Yahuar: blood (Midd., Yabar)	*Y. papa*: red blood potato	Paucartambo, Peru

* These words are used in both languages.

TABLE 11. (*d*) *Clothes*

Word	Examples	Locality
	Aymará	
Kahua: shirt (Bert., Cat.); poncho (Cev.)	*Pakko k. imilla*: lead shirt girl	Puno, Peru
	Quechua	
Punchu: poncho (Asc.) [the Indian blanket]	*Muru p.*: small poncho	Saquisilí, Ecuador
Huara: trousers (Midd., Ayacucho dialect)	*Jerga h.*: trousers of coarse cloth	Ayacucho, Peru
Chumpi: girdle or belt (Midd.); baby's binding strip or Indian belt (Cárd.)	*Corti ch.*: ?belt	Cochabamba and Achacachi, Bolivia

TABLE 12. (*e*) *Plants*

Word	Examples	Locality
	Aymará	
Tonko: maize (Bert., Mark., Mej., Cárd.)	*T. papa*: maize potato	Sucre, Bolivia
	T. pellu: maize ?	Santiago de Huata, N. Bolivia
*Chillca**: *Baccharis polyantha* (Herr.)	—	Paucartambo, Peru
Panti: flower (Cárd.) *Cosmos* sp.	*P. imilla*: flower girl	Achacachi, Bolivia; Puno, Peru
	Quechua	
Sisa: flower (Midd.)	*Yurac s.*: white flower	Abancay, Andahuailas and Ayacucho, Peru
	Ñutupa s.: small flower	Ayacucho, Peru
	Ritipa s.: snow-white flower	Ayacucho, Peru
Sacha: shrub, forest, low trees (Midd.); tree (Cárd.)	*S. papa*: tree potato [in Ecuador signifies wild potato]	Pichincha, Ecuador
Chaqui: stem, foot (Midd.)	*Juchuy ch.*: small stem	Ayacucho, Peru
Kora: herb, poisonous herb (Midd.)	*K. papa*: herb potato	Abancay, Peru
Chimbalo: berry (Asc.). [This is possibly not a Quechua word]	*Papa ch.*: potato grown from true seed†	Pichincha, Ecuador
	Ch. negra: black potato grown from berry	Pasto, Colombia
	Ch. morada: purple potato grown from berry	Pasto, Colombia
	Ch. blanca: white potato grown from berry	Pasto, Colombia
Chojllu: immature maize cob (Midd., Cárd., Gonç., etc.)	*Muru ch.*: small maize cob	N. Bolivia and S. Peru; Paucartambo, Peru
Uchu: chile, capsicum, ají (Midd., Mejía, Cárd., etc.)	*U.*: chile [See *Uchurumi in section dealing with tools and implements*]	—
Huillca: A tree whose fruit is used as a purgative (Midd.) *Piptadenia macrocarpa* (Cárd.) *Piptadenia columbina* (Herr.)	*H.*: huillca	Cuzco, Peru
Huairuru: *Cytharexylon Herrerae* (Herr.)	*H.*: huairuru	Yuncaipampa, Peru
Ormosia coccinea (Cárd., Herr.), a small tree whose seeds are red with a black spot at one end and are used for necklaces (Midd.)	*Alkka h.*: variegated huairuru	Cuzco, Peru
Chunta: hard-wooden palms of various species (Midd., Gonç.)	*Ch. chilla*: palm ?board	Santiago de Huata, Bolivia
Palms, especially *Bactris horrida*, a species with spines and very hard wood (Tasc.)	*Ch.*: palm	Cañar, Ecuador
Chihua: Cicadaceous plant with edible fruit, *Zamia chigua* (Tasc.)	*Ch. morada*: purple chihua	Azogues, Ecuador
Chillca: a shrub with bitter and glutinous leaves, *Baccharis* species (Gonç., Tasc., Herr.)	*Ch.*: *chillca*	Paucartambo, Peru

* These words are used in both languages.

† See Hawkes (1941, pp. 24–6) for a full account of this interesting process.

TABLE 12 (*cont.*)

Word	Examples	Locality
	Quechua (*cont.*)	
Sunchu: a shrub with yellow flowers (Midd., Gonç.) *Viguiera lanceolata* or *V. Mandonii* (Herr.) [Possibly so called because of yellow tubers reminiscent of the flower colour of this shrub.—J.G.H.]	*S.*: sunchu	Paucartambo, Cuzco and Abancay, Peru
	Paspa s.: russeted sunchu	Puno and Cuzco, Peru
	Alkka s.: variegated sunchu	Cuzco, Peru
Arracacha: *Aracachia esculenta* a plant belonging to the family Umbelliferae (Cárd.)	*A.*: arracacha	Cochabamba, Bolivia
Pfuña: fern (Yabar)	*Pf. sonko*: fern heart or core	Paucartambo, Peru
Murunga: a form of pepper (Asc.)	—	Ambato, Ecuador

TABLE 13. (*f*) *Foodstuffs, etc.* [*see also* (*e*) *Plants*]

Word	Examples	Locality
	Aymará	
*Ppitu**: milled toasted maize (Cárd.)	*P. huayakka*: sack of maize flour	Cochabamba and Eucaliptus, Bolivia
	Choque ppitu: potato flour	N. Bolivia, several examples
Kkati: boiled potatoes (Bert.), potatoes boiled with the skins (Cárd.)	*Kk. pinula*: boiled potatoes?	Copacabana, Bolivia
	Huila kk.: red boiled potatoes	La Paz, Bolivia
	Quechua	
Ttanta: bread (Midd., Cárd.)	*Tt. papa*: bread potato	Cochabamba, Bolivia
	Tt. huahua: bread baby†	Cochabamba, Bolivia
Kolli: a kind of sweetened bread (Midd.)	*K. blanca*: white sweetened bread	Cochabamba, Bolivia
	K. negra: black sweetened bread	Cochabamba, Bolivia
Cachi: salt (Midd., Gonç., Mej.)	*Puna c.*: puna salt	Cochabamba, Bolivia
Jakku: flour (Midd., Cárd., etc.)	*J. huayakka*: sack of flour	Puno and Paucartambo, Peru
Chupi: soup, stew (Midd., Yabar, Cárd., etc.)	*Ch. papa*: soup potato	Ayacucho, Peru
	Ch. socco: soup whitener	Paucartambo, Peru
Machcka: flour (Midd.)	*M.*: flour	Huancayo, Peru
	Yana m.: black flour	Huancayo, Peru

* These words are used in both languages. † See footnote to Table 8.

TABLE 14. (*g*) *Tools and implements*

Word	Examples	Locality
	Aymará	
Huislla: Wooden spoon (Cárd.)	*Huisllapaki*: spoon breaker (owing presumably to its hardness when cooked)	La Paz, Bolivia
Huayakka: sack (Cev., Cárd., Cat., Yabar)	*Pitu h.*: sack of maize flour	Cochabamba and Eucaliptus, Bolivia
	Jakku h.: sack of flour	Puno and Paucartambo, Peru
	Quechua	
Huarakka: sling (Yabar, Midd.)	*Nina h.*: red fire sling	Paucartambo, Peru
Huicu: a kind of stick (J.G.H.)	*H.*: stick	Huancayo, Peru
	Yana h.: black stick	Cuzco and Junín, Peru
Uchurumi: rounded stone for grinding chile or ají (Tasc., Cárd., etc.); hence, a hard, round potato	*U.*: grinding stone	Saquisilí and Riobamba, Ecuador
	U. negra: black grinding stone	Ambato and Cañar, Ecuador
	U. blanca: white grinding stone	Cañar, Ecuador

Table 15. (*h*) *Natural objects and phenomena*

Word	Examples	Locality
	Aymará	
Kunu: snow (Cev., Cárd.)	*Kunu-rana*: snow ?	Eucaliptus, Bolivia
Kala: stone (Cev., Bert.)	*Runa k.*: man stone	Tarija, Bolivia
Huarisalla: rock breaker (Bert.)	*H.*: rock breaker	Many localities in N. Bolivia
Tturu: clay (Cárd.)	*Poko tt.*: mature clay	Tiahuanaco, Copacabana and Achacachi, Bolivia
	Poko tt. huila: mature red, i.e. red clay in the right condition for use	Puno, Peru
	Quechua	
Kolla: the high cold part of the sierra (Midd.)	*K.*: from the kolla	Abancay and Andahuailas, Peru
Puna: the altiplano, high plateau (Midd.)	*P. cachi*: altiplano salt	Cochabamba, Bolivia
Orkko: hill mountain (Midd.); male (Midd., Cárd.). [The word 'mountain' indicates also that the potato to which it applies has wild affinities]	*O. amajaya*: mountain ?[see p. 217]	Puno, Peru
Ckocha: pond (Midd., Yabar)	*Ckellhua ck.*: gull pond	Paucartambo, Peru
Mayu: river (Midd., Asc.)	*M. rumi*: river stone, pebble	Abancay, Peru
Yacu: water (Midd., used in the north only)	*Y. rumi*: water stone, pebble	Latacunga, Ecuador
	Y. papa: watery potato	Pichincha, Ecuador
Unu: water (Midd.)	*U. kkompis*: watery ? [see Table 21]	Cuzco, Peru
Ckispi ingo: crystal (J.G.H.). [*Ckispi* = glass (Midd.)]	*Ck. i.*: crystal	Cuzco, Peru
Rumi: stone (Midd.)	*Mayu r.*: river stone, pebble	Abancay, Peru
	Yacu r.: water stone, pebble	Latacunga, Ecuador
Kalpa: worked earth (Midd.); rich soil (Cárd.)	*K. runa*: man from rich soil	Sucre, Bolivia
Riti: snow (Midd.); pure white (Cárd.)	*Ritipa sisan*: snow or pure white flower	Ayacucho, Peru
Nina: fire (Midd., Yabar)	*N. huarakka*: red fire sling	Paucartambo, Peru
Inti: sun (Midd., Yabar)	*I. chimacu*: sun ?	Paucartambo, Peru
Quilla: moon (Midd.)	*Janko qu.*: white moon	Puno, Peru

Table 16. (*i*) *Miscellaneous*

Word	Examples	Locality
	Aymará	
Pichuya: bundle, potatoes borne in groups of three or more (Cev., etc.)	*P.*: bundle	Cochabamba and Achacachi, Bolivia
	P. choque: bundle potato	Puno, Peru
	P. blanca: white bundle	Huarina, Bolivia
Huaycu: (applied to *Luki*) 'one hour', because the potatoes called *luki* take an hour to cook (Bert.) [see Table 21]	*H.*: one hour	La Paz, Bolivia
	Quechua	
Aca: dung, excrement (Midd., Varg., Herr.)	*Cuchi a.*: pig's dung	Cochabamba, Bolivia; S. and C. Peru (many examples)
Huañuchi: something that kills (Cárd.)	*Machu h.*: something that kills an old man or mule	Cochabamba, Bolivia
Paki: breaker (Yabar, Varg., Cárd.)	*P.*: breaker	Tunja, Colombia
	Cuchillo p.: knife or spoon breaker	Cuzco and Paucartambo, Peru
	Huisla p.: spoon breaker	La Paz, Bolivia

II. ADJECTIVES

TABLE 17. (*a*) *Colour*

Word	Examples	Locality
	Aymará	
Chiara: black (Bert., Cev., Cat., Cárd., etc.)	*Ch. imilla*: black girl	Many examples in N. Bolivia
	Ch. pala: black, flattened	Huatajata, Bolivia
	[Many other combinations]	[N. and C. Bolivia; Puno, Peru]
Janko: white (Bert., Cev., Cat., Cárd., etc.)	*J. imilla*: white girl	Many examples in N. Bolivia
	Parco j.: crooked, bent, white	Puno, Peru
	J. quilla: white moon	Puno, Peru
	[Many other combinations]	[N. and C. Bolivia; Puno, Peru]
Coyllu: white, applied to wool and white potatoes (Bert.)	*C.*: white	Cochabamba, La Paz and Tiahuanaco, Bolivia
	[Many combinations, especially with other words denoting colour. Probably the original meaning of this word has been lost]	Cochabamba, Bolivia
Pakko: lead coloured (Cev., Cárd.)	*P. kahua imilla*: lead shirt girl	Puno, Peru
Sali: grey (Cev.)	*S. chiar imilla*: grey black girl	Achacachi, Bolivia
Laram: blue (Garç., Mark., Vocab.)	*Parck l.*: crooked, bent blue	Puno, Peru
	Amajaya l.: ?blue [see Table 21]	Puno, Peru
	L. choque pfitu: purple potato flour	Eucaliptus, Bolivia
	[Many other examples]	[N. Bolivia; Puno, Peru]
Kkoyllu: dark blue (Cárd.)	*Kk. sotamari*: dark blue? [see Table 21]	Eucaliptus, Bolivia
*Culli**: purple	*Yana c.*: black purple	Cochabamba, Bolivia
	C. chimaco: purple? [see Table 21]	Paucartambo, Peru
Chupica: red (Midd., Cat., Cev.)	*Ch. imilla*: red girl	Puno, Peru
	Ch. yarama: red ?	Puno, Peru
Huila: red (Bert.); blood red (Cárd.)	*H. imilla*: red girl	N. Bolivia, many examples
	[14 additional combinations]	[N. Bolivia; Puno, S. Peru]
Chumpi: coffee coloured (Vocab., Midd.). [The word also signifies Indian belt]	*Ch. imilla*: brown girl	Cochabamba, Bolivia
Chitequet'†: spotted (Cev.)	*Ch. ulluco*: spotted ullucus (see p. 220)	Cochabamba, Bolivia
*Alkka**: interrupted (Midd.), variegated, two coloured (Midd.)	*A. imilla*: variegated girl	N. and C. Bolivia
	A. huarmi: variegated woman	Paucartambo, Peru
	[14 additional combinations]	[N. Bolivia; S. and C. Peru]
	Quechua	
Yana: black (Midd., Cárd., etc.)	*Y. imilla*: black girl	Puno, Peru
	Y. papa: black potato	Huancayo and Huancavelica, Peru
	[26 additional combinations]	[N. Bolivia; S. and C. Peru]

* In use in both languages.

† The apostrophe indicates an open sound, depending on the word following.

TABLE 17 (*cont.*)

Word	Examples	Locality
	Quechua (*cont.*)	
Yurac: white (Midd., Cárd., etc.)	*Y. imilla*: white girl	Cochabamba and Sucre, Bolivia
	Y. llusta: white, slippery	Cochabamba, Bolivia
	[19 additional combinations]	[N. and C. Bolivia; S. and C. Peru]
Riti: pure white (Cárd.)	*R. sisan*: pure white flower	Ayacucho, Peru
Okke: grey, ashen (Midd., Cárd., Varg.)	*O. charasamy*: grey ?	Paucartambo, Peru
	O. lomo: grey ? back	Cuzco, Peru
	O. muru chimacu: grey spotted	Puno, Peru
Pusi: grey (Yabar)	*P. conocito*: grey little cone (?)	Paucartambo, Peru
	P. ñahui: grey eyes	Saquisilí, Ecuador
Sokko: grey (Midd.); bleacher, whitener (Yabar)	*S. huakkoto*: grey? [see Table 21]	S. Peru
	Puca s.: red whitener	Paucartambo, Peru
	Chupi s.: soup whitener	Paucartambo, Peru
	S. toro: grey bull	Abancay, Peru
*Chejchi**: grey, ashen (Midd., Herr., etc.)	*Muru ch. pfuro*: spotted grey feather	Paucartambo, Peru
	Ch. paceña: grey, from La Paz	Cochabamba, Bolivia
Puca: red (Midd., Cárd., Yabar, etc.)	*P. imilla*: red girl	N. Bolivia
	[47 combinations with this word; it occurs more often than any other]	[C. and S. Bolivia; C. and S. Peru; Ecuador]
Kkellu: yellow (Midd., Gonç., Cárd., etc.)	*K. papa*: yellow potato (*S. goniocalyx*)	Ayacucho, Peru
	K. imilla: yellow girl	Sucre, Bolivia
	K. huakkoto: yellow? [see Table 21]	Paucartambo, Peru
Muru: spotted (Midd., Vocab.)	*M. ppalta*: spotted flattened	Andahuailas and Abancay, Peru
	Okke m. chimacu: grey spotted? [see Table 21]	Puno, Peru
	[Several other combinations]	[S. Peru; Ecuador]
Takko: Indian red (Gonç.)	*T. huaña*: Indian red, dry	Abancay, Peru

* In use in both languages.

TABLE 18. (*b*) *Shape and size*

Word	Examples	Locality
	Aymará	
Parko: crooked, bent (Midd., Garc.) [but see Table 21]	*P. janko*: white twisted	Puno, Peru
	P. larama: blue twisted	Puno, Peru
	Puca p.: red twisted	Paucartambo, Peru
	Quechua	
Ppalta: flattened (Midd.)	*Yurac pp.*: white flattened	Andahuailas, Peru
	Muru pp.: spotted flattened	Andahuailas and Abancay, Peru
	[Several other combinations]	[N. Bolivia; S. and C. Peru]
Suitu: long (Midd., Varg.)	*Puca s.*: red, long	S. and C. Peru, many examples
	Yurac s.: white, long	Cuzco, Peru
	[Many other combinations]	[S. and C. Peru; Ecuador]
Kkehuillu: somewhat twisted (Midd., Yabar)	*Yana kk.*: black twisted	Paucartambo, Peru
	Muru kk.: spotted twisted	Paucartambo, Peru
	Puca kk.: red twisted	Paucartambo, Peru
Ñutu: small (Midd.) [mashed (Cárd.)]	*Ñutupa runtu*: small egg	Ayacucho, Peru
	Ñutupa sisan: small flower	Ayacucho, Peru
Muru: cut off, short (Cárd.). [The same word also apparently signifies 'spotted']	*M. poncho*: short poncho	Saquisilí, Ecuador
	M. chaleco: short waistcoat	Abancay and Andahuailas, Peru

TABLE 19. (*c*) *Surface, texture, taste*

Word	Examples	Locality
	Aymará	
*Pfara**: dry (Bert.)	*Llusta pf.*: slippery, dry	Puno, Peru
Llusta: slippery (Cárd.)	*Yana ll.*: black, slippery	Cochabamba, Bolivia
	Puca ll.: red, slippery	Cochabamba, Bolivia
	Yurac ll.: white, slippery	Cochabamba, Bolivia
Huaña: dry (Bert., Cat., Mark., Cev.)	*H.*: dry	Puno, Abancay and Andahuailas, Peru
	Takko h.: Indian red, dry	Abancay, Peru
	Azul h.: blue, dry	Chincheros, Peru
	Yurac h.: white, dry	Chincheros, Peru
Ckeni: floury (Cev.)	*Ck. ahuachucha*: floury ?	Copacabana, Bolivia
	Ck. zapallu: floury gourd	Copacabana, Bolivia
	Suriman ck.: floury ? [see Table 21]	Achacachi, Bolivia
	Ck. amajaya: floury ? [see Table 21]	Copacabana, Bolivia
Pfiñu: sweet (J.G.H.). [The name seems to be generally applied to many varieties belonging to *Solanum stenotomum*]	*Pf.*: sweet	La Paz, Bolivia
Kkoso: delicate (Cev.)	*Kk. ñahui*: delicate eyes	Cochabamba, Bolivia
Janka: scabby (Bert.), tubers infected with the canker form of *Spongospora subterranea* (J.G.H.)	*J.*: scabby	Tiahuanaco and Achacachi, Bolivia
	Quechua	
Ppaspa: chapped (Midd.); russeted (J.G.H.)	*Pp. sunchu*: russeted sunchu	Cuzco and Puno, Peru
Katahui: watery (J.G.H.)	*K. negra*: watery, black	Cochabamba, Bolivia
	K. roja: watery, red	Cochabamba, Bolivia
	K. coyllu: watery, white	Cochabamba, Bolivia
Unu: watery (Midd.)	*U. kkompis*: watery ? [see Table 21]	Cuzco, Peru
Chaquillo: slightly dry (Cárd.)	*Yurac ch.*: white, slightly dry	Paucartambo, Peru
	Puca ch.: red, slightly dry	Paucartambo, Peru
Miskilla: rather sweet (Cárd.)	*M.*: rather sweet	Abancay, Peru
	Yurac m.: white, rather sweet	Paucartambo, Peru
	Muru m.: spotted, rather sweet	Paucartambo, Peru
	Yana m.: black, rather sweet	Paucartambo, Peru
	Puca m.: red, rather sweet	Paucartambo, Peru
Mallcu: bitter (Midd.). [In spoken Quechua *Kkallcu* means 'bitter']	*M.*: bitter	Chincheros, Peru
	M. rukki: bitter, wild	Paucartambo, Peru
Kkara: very salt or very bitter (Cárd).	*Kk. papa*: very bitter potato	Cochabamba, Bolivia
Mappa: stained, dirtied, blotched (Midd.), applied to potatoes infected with *Thecaphora solani* (J.G.H.)	*M.*: stained	Arequipa, Peru
Ckallhua: hardened (Yabar)	*Yana ck.*: black, hardened	Puno and Paucartambo, Peru
	Yurac ck.: white, hardened	Paucartambo, Peru

* In Quechua spelt *ppara* but also meaning 'dry'.

TABLE 20. (*d*) *Miscellaneous*

Word	Examples	Locality
	Aymará	
Kkosi: strong (Souk.)	*Kk.*: strong	Puno, Peru
Mulluncku: defective, faulty (Cev.) [applied to poor or weed types of potato—J.G.H.]	*M.*: defective	Eucaliptus, Bolivia
Poko: mature (Bert.)	*P. tturu*: mature clay	Tiahuanaco, Copacabana and Achacachi, Bolivia
	P. tturu huila: mature red clay	Puno, Peru
Pokoya: mature (Cev.)	—	Puno Peru

Table 20 (*cont.*)

Word	Examples	Locality
	Quechua	
Kkala: bare, naked (Midd.)	*Yana kk.*: black, bare	Ayacucho, Peru
Huira: fat (Midd.) [also = lard (Cárd.)]	*Hu. ppasña*: fat woman	Ayacucho, Peru
Machu: old (Midd.)	*M. huañuchi*: something that kills an old man or mule	Cochabamba, Bolivia
Orkko: male (Midd.), male or mountain (Cárd.)*	*O. amajaya*: male? [see Table 21]	Puno, Peru
China: female (Midd., Cárd.)	*Ch. amajaya*: female? [see Table 21]	Puno, Peru
	Papa ch.: female potato	Cañar, Ecuador

* In the sense of uncultivated, wild.

III. CLASSES OF POTATOES

Table 21

[*Note.* If found only in the literature and not collected by the author the authority is given in column 2.]

Name	Authority	Type of potato to which the name refers	Distribution
		Aymará	
Ahuachucha	—	'The best known and liked potatoes in this country' (Bert.)	N. Bolivia
Ajanhuiri	—	A class of frost-resisting potatoes (*Solanum Ajanhuiri*) of characteristic shape. The word may possibly be compounded from *ajano* = face (Bert.) and *huiri* = point of hard wood. Cev. gives *carantón*. According to Cárd. the word in vernacular Spanish means 'large face' or 'hideous mask'	Cochabamba, Eucaliptus, La Paz, Tiahuanaco and Huarina, N. Bolivia
Amajaya	—	'The best known and liked potatoes in this country' (Bert.). Cev. translates it as 'salted corpse'. The word is generally found coupled with colour or other descriptive adjectives, e.g. *A. larama* = purple *amajaya*, etc.	Tarija, Cochabamba and Copacabana, Bolivia; Puno and Paucartambo, Peru
Chapiña	—	'Purple potatoes from the flesh of which they are accustomed to make a dye' (Bert.). Gonç. also mentions this potato. A sample was obtained by me and found to have a jet black flesh. It is not known whether this variety is still in use for dyeing	Puno, Peru
Chiquiña	—	It is possible that this may be a corruption of *Chiquilla* q.v. (group IV, Table 22)	Puno, Peru
Huatoca	Bert.	'The best known and liked potatoes in this country' (Bert.)	?Peru; ?Bolivia
Jackayari	Bert.	(Spelt by Bert. *Hakhayari*.) 'Potatoes which greatly resist the frost' (Bert.)	?Peru; ?Bolivia
Kkami	—	A name generally applied to certain varieties of *Solanum stenotonum*. May be derived from *kkama* = dry hard (Bert.)	Tiahuanaco, Bolivia
Kkullukauna	Bert.	'The best known and liked potatoes in this country' (Bert.). [= 'log egg' (Cárd.)]	?Peru; ?Bolivia
Kusku	Bert.	'The best known and liked potatoes in this country' (Bert.)	?Peru; ?Bolivia

TABLE 21 (*cont.*)

Name	Authority	Type of potato to which the name refers	Distribution
		Aymará (*cont.*)	
Luki (=Luqui)	—	'Potatoes which greatly resist the frost' (Bert.). 'Somewhat bitter potatoes, but good for chuño' (Bert.). Applied to bitter potatoes belonging to the frost-resistant species *Solanum Juzepczukii* and *S. curtilobum*. The word does not mean 'bitter', but is applied to those classes of bitter potatoes used for making chuño. Many combinations, e.g. *Yurac l.*, *L. koillu*, *L. mari*, *L. pinko*, etc., etc.	Cochabamba, Eucaliptus, Hualata, Tiahuanaco, Achacachi and Santiago de Huata, Bolivia; Puno, Peru
Mari	—	A word that is never found alone but always combined, e.g. *Luki m.*, *Lauta m.*, *Huila m.*, *Chiar m.*, *Taka m.*, *Janko m.*	Tiahuanaco, Bolivia; Puno, Peru
Nayra ppoco	Bert.	'The best known and liked potatoes in this country' (Bert.) (*nayra*=eye)	Peru, Bolivia
Parkko	—	Applied exclusively to bitter varieties that are classified botanically with *Solanum Juzepczukii*. It would seem to be a slightly more northern equivalent of *Luki* (q.v.). Cev. translates it as *regodión* (?=joker); Garc. gives for *parco*, possibly a different word, the meaning 'one-eyed', perhaps on account of the small number of eyes on the tubers of this variety; Midd. in his *Die Aimará-Sprache* lists *parco* as 'crooked, bent'. Many examples, e.g. *P. janko*, *P. larama*, *P. chimaco*, etc. (see Table 18)	Puno and Paucartambo, Peru
Pfureja	—	Applied to certain early kinds of potatoes that grow at lower altitudes in N. Bolivia, classified botanically as *Solanum Phureja* and *S. Cardenasii*. Cev. translates it as 'arrival, coming', but this probably refers merely to the fact that it comes or matures early	Cochabamba, La Paz and Sorata, Bolivia
Pinku (Pingo)	—	A name also applied to *Solanum curtilobum* and *S. Juzepczukii*, possibly, as with *Luki*, having connotations with some bitter plant or principle. Bert. defines *pinco* as 'ridge beam of a roof', but it is difficult to see how this could be applied to a potato, and the words are probably different. Occurs alone and in combinations with colours, e.g. *Laram p.*, *Janko p.*	Cochabamba and Eucaliptus, Bolivia
Ppitiquiña	—	(Also spelt *ppitiquilla*, *ppiticana*.) Applied exclusively to varieties of *Solanum stenotonum*. The writer has never seen any attempts at translating this word, except that Bert. lists: '*ppatticalla*: The best known and liked potatoes in this country', and translates it as 'mantilla woven of diverse colours and (?) threads [talegas]'. The form *ppiticana* was found in two combinations, e.g. *Chiar pp.* and *Huila pp.*	Santiago de Huata, N. Bolivia
		Ppitiquilla was found twice	La Paz and Tiahuanaco, Bolivia
		Ppitiquiña occurred in many combinations, always with colours, e.g. *Puca pp.*, *Yana pp.*, *Yurac pp.*, etc.	Puno, Cuzco and Paucartambo, Peru
Sailulu	—	Translated by Cev. as 'lengthened', but is not mentioned in the dictionaries and is hence more probably a name given to a certain type of lengthened potatoes than an adjective of general use in the language	Cochabamba, Bolivia
Sakkampaya	—	Translated by Cev. as 'two weaknesses' (!) A class of long, cylindrical, white potatoes. Bert. gives *sakkapa*, 'a long fruit', and it is possible that this potato may have been named after a fruit whose original name is now lost	Potosí, Sucre, Eucaliptus, Cochabamba and Huatajata, Bolivia; Puno, Peru

TABLE 21 (*cont.*)

Name	Authority	Type of potato to which the name refers	Distribution
		Aymará (*cont.*)	
Sotamari	—	Translated by Cev. as 'overseer, foreman', but does not appear in the dictionaries. Occurs very commonly (13 times) in Bolivia, generally combined with adjectives of colour, e.g. *Huila s.*, *Laram s.*, *Alkka s.*, etc.	Eucaliptus and Cochabamba, Bolivia
Surimaña	—	'White and long potatoes' (Bert.); = 'buried, because tubers are borne at some depth' (Cev.). It is probable that Cev. has here only given a descriptive name and has not translated the original word. However, Garc. gives the word *suri* = 'ostrich'. It is tempting to connect the traditional head-burying of the ostrich with the translation by Cev., but too little is known as yet about this word for there to be any certainty in this surmise. The variant *surikahua* (= having the sight of an ostrich?) was found at Tiahuanaco, Bolivia	Sucre, Achacachi, Huarina and Tiahuanaco, Bolivia; Puno, Peru
		Quechua	
Chaucha	—	'The potato which matures in short time' (Gonç.); 'The early potato' (Midd.); 'Certain class of potatoes with yellow skin and floury flesh; small and early potato' (Tasc.). Most authors define the word as applying to types of early potatoes, one of these types having received the botanical name of *Solanum Chaucha*. Nevertheless, the *chauchas* from Colombia belong to a totally different species (*S. Rybinii*). No definition, other than those given above, has been applied to it with the exception of Cev., who translates it as 'money', 'small coin'. According to Cárd. this is a Chilean word in the first place. Many combinations occur	Huancayo, Tarma and Huancavelica, Peru; Saquisilí, Tulcán, Ambato, Cañar and Cuenca, Ecuador; Pasto, Colombia
Chimacu	—	A very common type of potato in S. Peru. The nearest translation I have been able to find is *cchimakha* = purple colour (Bert.), but this is probably a different word, since *Chimaco* generally occurs combined with various adjectives descriptive of colour, e.g. *Yurac ch.* (white *ch.*), *Yana ch.* (black *ch.*), *Okke muru ch.* (grey spotted *ch.*), etc.	Puno, Cuzco and Paucartambo, Peru
Huakkoto	—	'White large potato always used for soup' (Midd.). *Huakkotos*, although generally large, may be of any colour, as with *Chimaco*, e.g. *Kkellu hu.* (yellow *hu.*), *Sokko hu.* (grey *hu.*), etc.	Puno, Cuzco, Paucartambo, Abancay and Huancayo, Peru
Huata [*Guata* in Colombia]	—	A name applied to any late potato in contradistinction to the *chauchas* or earlies. Potatoes classed as *huatas* (or *guatas* as the word is sometimes spelt) also bear their ordinary varietal name. According to Cárd. the word *huata* means 'year'. It would probably be equivalent to our term 'maincrop', since in many parts of Ecuador and Colombia the main season's crop is called *de año* (year), signifying that this was the chief crop or harvest of the year. Tasc. also translates *guata* = year	Cañar, Ecuador; Ipiales, Pasto, Popayán, Cali and Manizales, Colombia
Kkompis	—	The word is applied to a class of potatoes probably identical with *Janko imilla* from Bolivia, isodiametric, with fairly deep, round eyes and non-coloured skin. It occurs only in Peru (with one exception from Cochabamba, Bolivia) and is very common. No translation is known	Puno, Cuzco, Paucartambo, Abancay and Andahuailas, Peru
Mahuai	Midd.	The early potato	—
Malkachu	—	A class of long, white potatoes, according to verbal information received by the author from Indians at Potosí	Tarija, Sucre and Potosí, Bolivia
Uri	Midd.	The early potato, called in Cuzco *Mahuai*, in Arequipa *Chaucha*	—

IV. GENERAL NAMES GIVEN TO POTATOES IRRESPECTIVE OF THEIR SPECIAL VARIETAL NAMES

TABLE 22

Word	Authority	Original spelling	Meaning
			Aymará
Chackiu	Bert.	*Cchakhiu*	Mixed potatoes of diverse kinds and colours
Chalu	Bert.	*Cchalu*	Mixed potatoes of diverse kinds and colours
Chara	Bert.	*Cchaara*	Bad potatoes of a given kind
Chiqui	Bert.	*Cchiqui*	Watery potatoes
Chiquilla	Bert.	*Chiquilla*	Selected potatoes from amongst the best of any given kind. [*Chucho ch.* and *Quero ch.* were obtained by me from Puno, Peru]
Ipi amkka	Bert.	*Ipi amcca*	Wild, very small potatoes [*amkka*=potato]
Ipina, Ipipa	Bert.	*Ipina, Ipipa*	Wild, very small potatoes growing in great numbers
Japu	Bert.	*Hapu*	Potatoes gathered at the time of sowing.
Janka amkka	Bert.	*Hanka amcca*	Potato which degenerates in quality. [Literally translated=scabby potato]
Kcati	Cárd.	*Kcati*	All coloured potatoes that are used for boiling.
	Bert.	*Ccati*	Boiled potatoes
Kea	Bert.	*Kea*	Potatoes which come up when the others are sown, by having remained below the earth
Kkea	Mej.	*K'ea*	Wild, or escaped potato.
*Kkipa**	J.G.H.	—	'Ground-keepers', plants from tubers left in fields from last year's crop (see also p. 218). [Obtained by me at Eucaliptus, Bolivia]
Kkochi	Bert.	*Ccochi*	Early potatoes
Llallahua†	Bert.	*Llallahua*	Monstrosities which grow like a hand, a balustrade or a head; monstrous potato, such as two potatoes joined together or like a hand
	Acosta	*Llallahua*	'There is a strange kind [of potato] they [i.e. the Indians] call *Llallahuas* which they kissed and worshipped'
Llullu	Bert.	*Llullu*	Potatoes remaining very small by reason of the frost [='immature' according to Cárdenas]
Lurama	Bert.	*Lurama*	Bad potatoes of a given kind
Pfiki papas	Bert.	*Phiki papas*	Potatoes remaining very small by reason of the frost [='immature' according to Cárdenas]
Queni	Bert.	*Queni*	Selected potatoes from amongst the best of any given kind
	Bert.	*Qhueeni*	Selected potatoes, or the best that there are of each kind
Ttumiri	Bert.	*Ttumiri*	Selected potatoes from amongst the best of any given kind. [This name was found twice by me in Puno and in Paucartambo, Peru]
Ulla talla	Bert.	*Ulla talla*	The best known and liked potatoes in this country
			Quechua
Cachu	Midd.	*Cachu*	Potato tubers left in the earth at harvest and which are beginning to sprout
	Gonç.	*Cachu*	
Chahua	Gonç.	*Chahua*	Raw potatoes

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* Originally Aymará word, now also used in Quechua.

† From the evidence given by Bertonio and Acosta it is probable that the Indians would set aside and venerate any potato tuber that grew in a peculiar and especially anthropomorphic shape. The worshipping of curiously shaped natural objects, not only potatoes, amongst the Indians was noted by several historians of the immediate post-conquest period.

TABLE 22 (*cont.*)

Word	Authority	Original spelling	Meaning
		Quechua (*cont.*)	
Ihua	Tasc.	*Igua*	Potatoes which grow from those left behind at th time of harvest. [Probably a local word confined t Colombia and of Chibcha origin]
Koyu	Gonç.	*Koyu papa*	Potatoes left in the earth at the time of harvest.
Muñi	Mej.	*Muñi*	Smaller potatoes from which *Uchu*, *Lokkro*, etc. i made. [These are two kinds of stew.—J.G.H.]
Putu	Gonç.	*Putu*	Potato tubers left in the earth at harvest and whic are beginning to sprout
Yura	Midd.	*Papa yura*	Potato plant [i.e. the haulm]

V. WORDS CONNECTED WITH POTATO CULTIVATION

(Taken from Dictionaries and Vocabularies)

TABLE 23

Word	Authority	Original spelling	Meaning
		Aymará	
Amkkachasitha	Bert.	*Amccachasitha*	To gather a portion of the potatoes befor they are well matured
Amkkachatha	Bert.	*Amccachatha*	
Iñacatha	Bert.	*Iñacatha*	To dig up potatoes without rooting up th plant
Luntatha	Bert.	*Lantatha*	To dig up potatoes after sowing or for othe causes or disputes [i.e. to steal sow potatoes (Cárd.)]
Makuncara	Bert.	*Makuncara*	The potato berry
Piu irutatha	Bert.	*Piu irutatha*	To look at a handful of the potatoes in orde to find out if the year will be a good o a bad one; that is a great superstition
		Quechua	
Jallppina	Midd.	*'Hallp' ina*	Hoe for digging up potatoes
Jallppiy-pacuy	Midd.	*'Hallp' iy-pacuy*	To dig up potatoes by day labour
Papa allana	Midd.	*Papa allana*	Potato digging implement
Papa chajra	Midd.	*Papa chajra*	Potato field
Papa jallppiy	Midd.	*Papa 'hallp' iy*	Potato harvest
Runa papata jallppin	Midd.	*Runa papata 'hallp' in*	The man digs the potatoes out of the ground [According to Cárdenas this should mean He who digs the *Runa* variety of potatoes
Usu	Forbes	*Usu*	Disease. [Applied to potatoes collected by me that were infected with Aucub mosaic virus]

APPENDIX

Alphabetical list of words whose meanings have not been ascertainable

(See also group III, Table 21)

Word	Combination	Notes	District
Achspa	*A. papa*	'Wild potato' (see Table 3), but exact translation and language unknown	Pichincha, Ecuador
Almilla	*Puca a.*	?corruption of the Aymará word *imilla* = girl, but in a Quechua-speaking district	Tampumachay, nr. Cuzco, Peru
Apacana	—	—	Cochabamba, Bolivia
Bandurandis	—	—	Tampumachay, Peru
Batucara	—	—	Cañar, Ecuador
Calvachi	—	—	Saquisilí and Ambato, León, Ecuador
Camara	—	This does not appear to be the Spanish word *cámara*	Cochabamba, Bolivia
Camaranchi	—	—	Chincheros, Peru
Cambrus	—	—	Ayacucho, Peru
Canasulla	*C. koillu*	—	Cochabamba, Bolivia
Canchiri	—	—	Cochabamba, Bolivia
Carlosa	—	—	Cochabamba and Eucaliptus, Bolivia
Cashpa	*C. papa*	(*Gaspar papa*—probably a variation of *Cashpa papa*—was found at Huancavelica, Peru)	Ayacucho, Peru
Charasany	—	—	Paucartambo, Peru
	Okke ch.	Grey —	Paucartambo, Peru
Chaulki	—	—	Copacabana, N. Bolivia
Chava	—	A weed potato	Lake Tota, Boyacá, Colombia
Chimbalan, *Chimbalo*	—	Potato grown from true seed; actually = *berry* (but from what language?)*	Pichincha, Ecuador; Pasto, S. Colombia
Chirisaya	*Ch. luki*	—	Achacachi, N. Bolivia
Chistiri	*Ch. koillu*	—	Cochabamba, Bolivia
Chohuahuisca	—	—	Puno, Peru
Chohuajineca	—	—	Puno, Peru
Chokko	—	—	Achacachi, N. Bolivia
Chuclo	*Ch. chiquilla*	—	Puno, Peru
Chuga	*Chaucha ch.*	—	Cañar, Ecuador
Chugua	—	Applied to *Ullucus tuberosus*	Bogotá, Colombia
Churrusqui	—	Probably all three words are variations	Abancay, Peru
Churuspi	*Yana ch.; puca ch.*		Paucartambo, Cuzco and Puno, Peru
Churuspiña	—		Paucartambo, Peru
Chuya	*Ulla ch.*	—	Saquisilí, León, Ecuador
Cipi	*C. ñahui*	— eye	Cochabamba, Bolivia
Ckañari	—	Doubtful whether this could refer to the Ecuadorian province of Cañar	Abancay, Peru
Ckihuisilla	—	Possibly from *Kaisalla* (q.v.)	Cochabamba, Bolivia
Ckulli	*Puca ck.*	—	Cochabamba, Bolivia
Cochicallo	—	—	Puno, Peru
Corti	*C. chumpi*	?Spanish *corto* = short	Cochabamba, Bolivia
Cubio	—	Applied to an *Oxalis* species	Zipaquirá, nr. Bogotá, Colombia

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* This may be a word from the Barbacoan languages of north-west Ecuador and south Colombia (see Jijón y Caamaño, 1919, p. 22).

Word	Combination	Notes	District
Culluna	—	Translated by Gonçalez Holguín as 'potato clamp'	Abancay, Peru
Curiquinga	*Chaucha c.*	?=a species of bird	Pasto, S. Colombia
Espincui	—	—	Chincheros, nr. Cuzc Peru
Garmendia	—	—	Chincheros and Cuzc Peru
Gulupa	—	—	Tunja, Boyacá, Colombia
Hualera	*H. kana*	—	Paucartambo, Peru
Huallas	—	—	Huancayo, Junín, Peru
Huanouri	—	—	Achacachi, N. Bolivia
Huarisaya	—	—	Tiahuanaco, Achacachi, etc., N. Bolivia
Huatay	*H. pancho*	?=worked	Paucartambo, Peru
Huecco	—	Perhaps *huicu*=a stick	Huancavelica, Peru
Huicuto	—	—	Huancayo, Peru
Huinchina	—	?=hair band	Ayacucho, Peru
Huiruntos	—	—	Cuzco, Peru
Ikkari	—	—	Cochabamba, Bolivia
Incalo	—	—	Chincheros, Peru
Jahuilumuchi	—	—	Paucartambo, Peru
Janu	*J. ccallo*	—	Abancay, Peru
Jenchu	*Choke j.*	Potato —	Huarina, N. Bolivia
Juare	*J. ppalta*	— flattened	Abancay, Peru
Junurana	—	—	Cochabamba, Bolivia
Kahuisillo	*K. negro*	*Kahui*=fruits dried in the sun (Midd.)	Cochabamba, Bolivia
Kaisalla	—	Applied to bitter potatoes classified as *Solanum Juzepczukii*	Eucaliptus and Tiahu naco, N. Bolivia
Kamara	—	—	Tiahuanaco, N. Bolivia
Kamisaya	—	Perhaps from *camisa*=shirt	Cochabamba, Bolivia
Kana	*Hualera k.*	?plaited (Cev.)	Paucartambo, Peru
Kkanchalli	*Azul kk.*	—	Paucartambo, Peru
Kkekkena	*Culli kk., Yurak kk.*	Purple, white —	Paucartambo, Peru
Kkekkerana	*Huarmi kk.*	?frivolous woman (Yabar)	Paucartambo, Peru
Kkohuasa	—	—	Paucartambo, Peru
Kkoulla	—	Possibly *ccolla*, from the province of that name	Cochabamba, Bolivia
Kkoyu	*Kk. ñahui*	?=bruised eye	Cochabamba, Bolivia
	Kk. juana	?=bruised —	Abancay, Peru
Kkusi	—	Sometimes translated 'joy'	Chincheros, nr. Cuzc Peru
	Puca alkka kk.	Red spotted *kk.*	Paucartambo, Peru
Koko	*Talca k.*	Perhaps from *koka*=tree (Midd., Ay.)	Puno, Peru
Kutilo	—	—	Huancayo, Peru
Labrabi	—	—	Achacachi, N. Bolivia
Lanta	*L. mari*	—	Puno, Peru
Lapiya	—	Also spelt *Lappía*	Cochabamba, Bolivia
Lari-ajou	*L. koillu*	?an article of clothing	Cochabamba, Bolivia
Laurahui	—	—	Achacachi, N. Bolivia
Lekke	*L. chaqui*	— dry	Paucartambo, Peru
Lekkori	—	—	Cochabamba, Bolivia
Linlijo	—	—	Abancay, Peru
Lisaraza	—	— ?smooth	Central Colombia, ver frequent
Llaca	*Huakkoto ll.*	— lean meat?	Cuzco, Peru
Lloke	—	—	Huatajata, N. Bolivia
Locumba	*Runa l.*	Man —	Cochabamba, Bolivia
Lunca	*Puca l.*	Red —	Cochabamba, Bolivia
Luntusa	—	—	Puno, Peru
Morockeri	*Luki m.*	—	Eucaliptus, Bolivia
Moronquis	—	—	Huancavelica, Peru
Nocha	—	—	Cochabamba, Bolivia
Pakkocha	*P. huma*	—	Paucartambo, Peru

Word	Combination	Notes	District
Pala	*Chiar p.*, *Huila p.*	Black or red? rope	La Paz, Tiahuanaco and Huatajata, N. Bolivia
Palama	—	? = flat	La Paz, Potosí, etc., Bolivia
Pali	*Puca p.*	—	Sucre, Bolivia
Pancho	*Huatay p.*	—	Paucartambo, Peru
Paspuella	—	—	Carchi, N. Ecuador
Pellu	*Tonko p.*	Maize —	Santiago de Huata, N. Bolivia
Pichi	*P. suitu*	? red long, or long root	Ayacucho, Peru
	Pichihua	? *pichuya* = a bundle	Cochabamba, Bolivia
Pihuan	*P. huakkoto*	—	Cuzco, Peru
Pinahua	*P. choke*	— potato	Puno, Peru
Pinula	*Kcati p.*	— boiled potatoes?	Copacabana, N. Bolivia
Piñazo	—	?from *piña* = a pineapple	Puno, Peru
Pitoca	—	—	Tiahuanaco, N. Bolivia
Poyhuan	*Conocito p.*	? = heart (applied to animals)	Cuzco, Peru
Ppicke	*Like-Like-pp.*	—	Puno, Peru
Ppicochara	—	—	Puno, Peru
Ppujño	—	—	Puno, Peru
Pujeri	—	—	Huatajata, N. Bolivia
Puli	*Muru p.*, *Puca p.*	—	Paucartambo, Peru
Puñash	—	—	Junín, Peru
Pusu	*P. ñahui*	— eye	Saquisilí, León, Ecuador
Putis	—	—	Ayacucho, Peru
Quero	*Qu. chīquilla*	Probably from a certain type of vessel of that name found originally at Tiahuanaco	Puno, Peru
Queulla	—	*Quella* = iron (Ay. Cat.)	Tarija, Bolivia
Quinche	—	Possibly from *quencha* = enclosure, wall, barrier (Tascón), or from a place-name in Ecuador	Bogotá, Colombia
Recran	—	—	Huancayo, Peru
Sailulu	*S.*, *S. blanco*, *S. colorado*	? = lengthened	Cochabamba, Bolivia
Sahuasiray	—	—	Paucartambo, Peru
Sakkta	*S. mate*	—	Huancavelica, Peru
Sanso	—	—	Abancay, Peru
Sari	*S. papa*	Perhaps *sara* = maize	Huancavelica, Peru
Secha	—	—	Tiahuanaco, Bolivia
Selo	—	—	Saquisilí, León, Ecuador
Sicasta	—	—	Huancayo, Peru
Sihuanco	*S. choke*	? = wild potato	Puno, Peru
Siki	*Puca s.*	? = buttocks	Cochabamba, Bolivia
Simucu	*S.*, *Alkka s.*	— variegated	Puno, Chincheros and Abancay, Peru
Sipancachi	—	—	Potosí, Bolivia
Sonsa	*S. imilla*	— girl	Sucre, Bolivia
Suamanchachi	—	'Frightens robber' (Yabar)	Paucartambo, Peru
Susu	—	—	Abancay, Peru
Taca	*T. papa*, *T. mari*	—	Cochabamba and Tiahuanaco, Bolivia
Tacanguilla	—	—	Saquisilí, León, Ecuador
Tajami	—	—	Paucartambo, Peru
Talca	*T. koko*	Probably a shortened form of *tallaca*	Puno, Peru
Tallaca	*Alkka t.*	Probably a corruption of *talega* = bag or purse (Sp.)	Cuzco, Peru
Taquiña	—	—	Cochabamba, Bolivia
Tarako	*Huila t.*, *Chiar t.*	Red and black?	Achacachi, N. Bolivia
Tarquina	*T. imilla*	Possibly from *taquina*	Eucaliptus, Bolivia
Thalaco	—	Possibly a corruption of *tallaca*, q.v.	Abancay, Peru
Thuima	*Th. luki*	— bitter	Puno, Peru
Tinackoya	—	—	Cochabamba, Bolivia

Word	Combination	Notes	District
Tinya	*Kkalla t.*	Parrot (?) tambourine	Abancay, Peru
Toracari	—	—	Cochabamba, Bolivia
Ttele	—	? = intoxicated (Yabar)	Paucartambo, Peru
Ttoclolo	*Puca tt., Kkellu tt.*	Red, yellow —	Paucartambo, Peru
Tune	*T., Papa t.*	—	Tilcara, Argentina
Tuni	*T., T. paula*	—	Cochabamba, Bolivia; Puno, Peru
Ula	*U. chuya*	(See *Ulla talla*, Table 22)	Saquisilí, León, Ecuador
Ullasaya	—	—	Paucartambo, Peru
Unchuna	—	—	Paucartambo, Peru
Utcucuri	*Yurac u., Yana u.*	White, black —	Puno, Peru
Uytulu	*Luki u.*	Bitter —	Cochabamba, Bolivia
Yarama	*Chupica y.*	Red —	Puno, Peru
Zhio	—	A weed potato	Azogues, S. Ecuador
Zimoquita	—	—	Copacabana, Bolivia
Zulto	—	—	Cochabamba, Bolivia
Zutaco	—	—	Puno, Peru

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Some Suggestions on the history of Potato Virus *X*. By J. E. van der Plank, Division of Botany and Plant Pathology, Pretoria. (Communicated by Dr J. Ramsbottom, O.B.E., F.L.S.)

[Read 20 January 1949]

Introduction

When Johnson (1925) found that the sap of potatoes which were apparently healthy, or which showed only a faint mottle on the leaves, was able to infect tobacco and other plants, he made the first contribution to the recorded history of potato virus *X*. What was its early history? As the virus had permeated potato stocks to such an extent that no clone of any of the standard North American varieties of that time could be found free from it, and most British varieties, excepting a few which are immune, were in nearly as bad a state, it seems to have been fairly generally accepted that the virus had had a long history in the potato. For example, Salaman (1939), in the most authoritative account we have of potato virus *X*, expresses the view that the virus has been with the potato for an indefinite time, possibly since it was first cultivated as a field crop in Europe. But evidence collected since 1939 leads to a very different conclusion. We do not know the history of the virus in the potato's native home, South America; but so far as Europe and South Africa are concerned, the virus appeared to become destructive only in this century, and, if it existed previously at all, it was of little account. The virus probably came into stocks as a result of comparatively recent changes in the potato industry, and is, we believe, a misfortune of our own making. The evidence is necessarily indirect, since there are no records previous to the discoveries of Johnson in 1925, and comes from a diversity of items: from the potatoes of Basutoland and Tristan da Cunha; from tests with the variety 'Up-to-Date' and, perhaps, 'Champion'; and from the general history of the potato, especially in relation to the abundance and longevity of varieties. Taken alone, the evidence of several of these items may seem flimsy, but together they tell a consistent story of the modernity of the virus as a destructive agent in the domestic potato.

The 'native' potatoes of Basutoland

In 1833 the Chief of the Basuto, then a young tribe in territory far distant and well isolated from any white settlement, asked for missionaries to work among his people. The Rev. E. Casalis and two companions of the Paris Evangelical Missionary Society responded. After selecting a suitable site for the mission, Casalis went by ox-wagon to Phillipolis, about 150 miles away and also a missionaries' outpost in the wilds, to collect his belongings, and took the opportunity to acquire cuttings of fruit trees, vegetable seeds, and 'especially potatoes'. With these he returned to Basutoland, started a nursery, and distributed his plants among the Basuto. This is described in his autobiography, *My Life in Basutoland* (English translation by J. Brierley, Religious Tract Society, London, 1889). The Basuto developed into a strong tribe, spreading along the foothills and valleys of the mountains, and as they spread they carried their potatoes with them. At no time did they use potatoes as an important article of food—their crops are mostly maize, Kaffir-corn, wheat and peas—but they kept them in cultivation, and kept them surprisingly pure. Outside small kitchen gardens, potatoes grow among maize, in fallow fields and almost anywhere that land has been broken up. There are more than a dozen varieties including at least six with passably good yields. Modern varieties are rare among them, and it is remarkable that 'Up-to-Date', which has been grown for half a century round the borders of Basutoland in what is now the Union, was not seen in a 'wild' state. Isolated in a mountainous country, the Basuto continue to grow what is virtually a pure relic of the potato industry as it existed more than a hundred years ago, with varieties that tally with the general description of potatoes at that time.

What concerns us is that several hundred tubers of these 'native' potatoes have been tested without finding a trace of virus *X*. It is only when they have been grown beside modern varieties, in experimental plots or kitchen gardens, that the virus is found. Several of the varieties were tested, and all proved susceptible on inoculation. They are healthy, therefore, only because they have not been in contact with the virus, and, on the evidence to be presented later that infected clones retain their infection without loss from generation to generation, must have been healthy when they were introduced.

In Casalis's time, Phillipolis was an outpost of the Eastern Cape Colony, where we know from the old agricultural census there was quite a flourishing potato industry in the 1830's. The chief centre seems to have been the Albany district, the headquarters of the 1820 settlers from Britain. One cannot go so far as to say that the varieties at that time were British, but it would be fairly safe to say they were European, which is substantially all that concerns us now. The South African industry has probably always been, and still is, an off-shoot of potato culture in other lands.

We take the evidence from Basutoland to mean that virus *X* was rare in Europe at the beginning of the nineteenth century, if it existed at all. Against this reading two objections might be made. It might be assumed that sometime during their long history in Basutoland, potatoes had been raised sexually from true seed. There is no evidence of this. Initiative in agriculture is not among the Basuto virtues. The Basutos lack the incentive to improve what is to them a very minor crop, and are without glasshouses for use in the cold dry winter. Moreover, the main varieties seem to be distributed throughout the length and breadth of the Protectorate, without evidence of the localization which would probably follow efforts at breeding in that very scattered community. That a few natural seedlings may have arisen is quite possible, but we are concerned only with the possibility of a considerable replacement of old varieties by new. Of that, there is no evidence. As a second objection, it might be observed that the plants are grown under conditions of great dispersion, and it might be assumed that infected plants were originally present but died out as a result of the natural selection, in the Darwinian sense, of healthy clones. We may answer this by a supposition. Suppose one were to buy seed at random on the market, say 'Up-to-Date' or 'Arran Chief' on the South African market, or 'Kerr's Pink' or 'Majestic' in Britain, or 'Irish Cobbler', 'Triumph', 'Green Mountain' or 'Katahdin' in the United States. Is it likely that after 100 years, or any other period, the potatoes would be free from virus *X*? This might happen with one or two varieties like 'Katahdin', but one cannot believe that all would be healthy, for the very good reason that most of the samples would have contained no healthy tubers in the first place. If the Basuto potatoes are all healthy now, it can only be because they were all, or almost all, healthy when they were brought in.

THE POTATOES OF TRISTAN DA CUNHA

From Tristan da Cunha, about midway between the Cape and South America, comes evidence to support that from Basutoland.

In 1816 a garrison from the Cape landed at Tristan da Cunha, which was regarded as an outpost of St Helena, where Napoleon had just been sent. At that time the island was not as lonely as it was afterwards to become. The South Atlantic had a great whaling industry, and the seas around Tristan da Cunha were described as being alive with whalers from New Bedford, Mass. Moreover, Tristan da Cunha was on the trade route from Europe to the Cape; clippers following the wind often passed, and, although they rarely called, the islanders came off in their boats to exchange commodities. Whaling ended about 1850, and the island became completely isolated when steam ousted sail twenty or thirty years later. From then, until 1939, when a weather station was built, the only contacts that the few score islanders had with the rest of the world, were through occasional visits by warships from Simonstown. These were rare, at intervals of a year or, generally, longer.

When the Cape garrison landed at Tristan da Cunha in 1816, they intended to plant wheat, but there is no record of this being done. Eight years later, bread was practically unknown—this on the authority of the artist Earle who was marooned there for nearly a year—but potatoes were abundant, of the finest flavour, and formed the chief article of food and traffic. Until the last War, the position remained unchanged. No other crops were grown and, except for small quantities of flour landed from passing ships, the islanders were forced to live mostly on potatoes, fish and sea-birds' eggs. The Irish, even before 1845, were never so dependent on the potato crop.

Two varieties of potato seem to be grown: a pink-skinned and a white-skinned. The white-skinned variety, in particular, is of an old type, with numerous deep eyes and the general appearance of potatoes described in Europe in the first half of the nineteenth century. It would seem a hopeless task to trace their origin. The island in the early nineteenth century had close connexions with the Cape, with Europe, and (through the whalers) with North America, and any of these might have provided the potatoes in the first place.

I was given two fairly large samples of the pink-skinned variety, and a small sample of the white. They were free from virus *X*. This is evidence which fits in very well with that from Basutoland. In Basutoland there are a number of varieties, not valued very highly as food, scattered extensively among the mountains; in Tristan da Cunha, the potatoes, the main supply of food, are grown in a concentrated area in the most intensive way, and if virus *X* had been present it would have had ideal conditions in which to spread.

It is sad to have to record that the island's freedom from virus *X* is probably a thing of the past. Recently, during the War, quantities of seed potatoes were shipped from the Cape at a time of shortage on the island. They must inevitably have taken the virus with them, and it can only be a matter of years before the old stocks suffer. Needless to say, no plant pathologist was consulted before the recent shipments of potatoes went to Tristan da Cunha. By the greatest of good fortune no blight appears to have been shipped with the potatoes; and the island seems still to be blight-free in a climate which would be perfect for *Phytophthora*.

THE EVIDENCE OF 'UP-TO-DATE'; THE CASE OF 'CHAMPION' AND OF THE MODERN VARIETIES

More recent evidence is given by 'Up-to-Date'. This was one of the varieties examined in some detail when attention was first given to virus *X* in Britain, towards the end of the 1920's and early 1930's. No plant could be found which was not infected, and from the scope of the tests it is clear that in Britain by 1930 the variety was almost completely infected with the virus.

In Australia infection was slower. In 1936 one tuber out of 500 examined and in 1940 twenty-eight tubers out of 960 were found free from virus *X* (Bald & Norris, 1941). More recently Bald (1944*a*) recorded that clones derived from single-plant selections by Dr R. A. Scott in Tasmania proved to be virus-free, a truly remarkable achievement.

In South Africa the first tests were made a few years ago on over 2000 tubers from a crop grown from seed imported from various sources in Scotland and Northern Ireland. Every one was infected. This confirmed that British stocks are for all practical purposes entirely infected. It also demonstrates that, unlike some viruses, potato virus *X* is not cast off, or only to a very slight extent, by an infected plant, so that a diseased clone remains diseased for ever. This fact has already been used in the discussion of the potatoes from Basutoland, and will be used again. Another attempt was made in 1942 by Mr P. G. C. Brett (formerly of the Division of Botany and Plant Pathology, Pretoria), this time with material that had been in South Africa for many generations. Among just under 1000 tubers, five were found uninfected. The origin of this stock could be traced with certainty. It came from Scotland in 1929, and had been grown since by Mr W. H Greathead on Woodbush Mountain. Perhaps because the stock survived for several years as groundkeepers on fallow land, it retained a few healthy plants to prove that in 1929 there were still uninfected clones in Britain.

That 'Up-to-Date' in Britain was very heavily infected, but not completely overrun by the virus in 1929, suggests that the variety became infected in about the middle of its career. It was introduced in 1893. Had it been infected very early, there would have been little chance of healthy tubers surviving as long as they did, if one may judge by the fair speed at which the virus spreads through stocks of this variety; while the possibility of late infection is excluded by the prevalence of the virus during the last twenty years. The evidence would not be inconsistent with the view that virus *X* was still uncommon in 'Up-to-Date' about 1910, that it was common enough to be seriously destructive about 1920 and that it had reached the point of being almost universal about 1930. We allow here roughly ten years for the virus to pass from the stage at which it does little damage, even if it is present, to the stage at which the variety is badly affected. Some figures on this point are given by Clinch, Loughnane & Murphy (1938). They found that crops of the maincrop[1] varieties 'Champion' and 'Arran Banner', believed at the time of planting in 1928 to be virus-free, but subsequently suspected of having contained foci of infection, revealed 38–94 % of latent infection after they had been grown in isolation in Donegal for five to seven years. Other figures have been given by Loughnane & Murphy (1938). Of fourteen healthy plants interplanted between infected plants in the field, only two became infected. In another experiment, in which the plants were grown in a glasshouse and the foliage kept moving in a current of air from a fan, eight plants which were interplanted between diseased plants became infected out of twenty-seven. At Rothamsted, Roberts (1946) found that in no year did more than one plant in ten in contact with infected plants become infected. Results of much the same order have been obtained in South Africa under very different climatic conditions. In a row of 200 'Up-to-Date' plants containing twenty infected plants, scattered at roughly equal intervals among 180 healthy plants, only six became infected during the season, all six having been in direct contact with infected plants. With 'Dunbar Standard', two plants became infected during the course of the season after planting a random mixture of twenty healthy and ten infected tubers. We shall use one of these sets of results—that six of the plants on either side of twenty infected plants acquired infection during the year—to calculate roughly how infection mounts during the course of years. If one postulates that infection comes only from plants which were infected at the start of the season, that it spreads only by direct contact between neighbours in a row and does not cross from row to row, and that a plant between two diseased plants has twice the chance of becoming infected as one in contact with only one diseased plant, infection may be expected to increase from 10 to 20 % in three years, to 50 % in the eighth year, to 80 % in the thirteenth and to 90 % in the fifteenth[2] year. This agrees with the allowance of approximately ten

[1] It is probably pertinent that one should compare maincrops with maincrops and earlies with earlies. Virus *X* spreads from plant to plant by contact of the foliage, and one would expect it to spread faster in maincrops, with their more abundant foliage and longer period of growth, than in earlies. There is no evidence that immunity, as in 'Epicure', or resistance, as in 'Katahdin', is related to maturity; and nothing is implied except that, susceptibilities being equal, the annual increases of infection will be greatest in late varieties.

[2] On these postulates, which for a fair approximation neglect the possibility of infection spreading between rows or, chain-like, from plant to plant along a row, the number of plants becoming infected during the season is $2p\left(\mu-\frac{\mu(\mu-1)}{n}\right)$ or, for long rows, simply $2p\left(\mu-\frac{\mu^2}{n}\right)$, in which n is the total number of plants in the row, μ the number diseased at the start of the season, and p (in this case 6/40 the probability that a plant in contact with one infected plant at the start of the season will itself become infected. These formulae may be derived from the equations given by van der Plank (1946

years for the disease to increase from a point at which it is scarcely harmful, roughly 20 % to one at which the harm is great, roughly 80 %. (To carry the calculation further as an interesting aside, infection would increase from 10 to 99 % in the twenty-second year, and to 99·9 % in the twenty-ninth year. A few odd tubers survive for many years, which may explain why it has been possible with all old British varieties to find at least a few healthy clones with which to build up virus-free stocks.)

It is largely on the history of the variety that the second decade has been suggested as the time when 'Up-to-Date' became badly infected. The fate of minor varieties may depend on fashion or chance. But 'Up-to-Date' was perhaps the greatest variety ever bred in Britain, and deservedly achieved a popularity—whether measured by its dominance over other varieties, by the parts of the world to which it spread, or by the number of synonyms by which it was known—not attained by any variety before or since. Any change in its fortunes were, therefore, likely to have had real significance. In 1910 it had an unchallenged position among maincrops in Britain; by 1920 it had declined, and was swiftly going out of production. There are thus two sets of evidence: evidence from tests for the virus which suggests that 'Up-to-Date' was infected round about its middle life, probably about the second decade of the century, possibly a little earlier but certainly not much later; and the evidence of actual history that the variety declined badly between 1910 and 1920. There is surely good reason for connecting the evidence, and for assuming that infection by virus *X* was the cause of the decline; the history of the decline fixes the time of serious infection as between 1910 and 1920. The alternative to this is the improbable assumption that the two acts of evidence are unrelated, that 'Up-to-Date' declined between 1910 and 1920 for some unexplained reason unrelated to its health, and that at some slightly earlier date the variety was infected but did not suffer the loss of popularity or productivity which one would expect from the known facts about the effect of virus *X* on yield.

The selection of the period, 1910 to 1920, for the infection of 'Up-to-Date' is thus a matter of likelihood. It fits all the known facts, and conflicts with none. Its importance for our purpose is that in 1910 'Up-to-Date' was seventeen years old as a commercial variety (which does not include the many years of its existence before it was released by its breeder), and for it to have survived so long without serious infection (assuming our previous deductions are correct) indicates that there was not much infective material in existence. One cannot believe that a modern susceptible maincrop would escape for that period. Most have a fairly heavy infection within a few years of, and even at the time of, their release. Figures are not available for the progress of infection in new varieties, but observations show a fairly general distribution of the disease among comparatively young maincrop varieties. The tests made by Scott (1938) show that 'Arran Peak' carried appreciable infection when it was introduced in 1936–37—and seems now, within ten years of its release, to be almost completely overrun—while the experiments of Clinch *et al.* (1938), were begun soon after 'Arran Banner' was put on the market in 1926–27. Among United States varieties, the position seems much the same. Judged by small and possibly not very representative samples, 'Sebago' and 'Potomac', introduced in 1938 and 1943 respectively, and 'Menominee', just introduced, are heavily infected. 'Katahdin', introduced in 1932, seems to have escaped serious infection, but this

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for estimating runs of two or more diseased plants in contact with one another. It is evident that in long rows infection spreads at a maximum rate when 50 % of the plants are infected.

The third postulate, that a plant between two diseased plants has twice the chance of becoming infected as one in contact with only one diseased plant, is only a simplification. All one may reasonably postulate is that there will be twice the mean number of transfers of virus to such a plant, from which one may calculate with the help of the Poisson theorem that the probability of the plant becoming infected during the season is $2p-p^2$. The corrected postulate makes calculations cumbersome, and is not very necessary except for high values of p. The corrections are greatest when the bulk of the plants are infected. In the example, given above, the experimental estimate of p has not the accuracy to warrant the refinement of the correction.

variety is abnormal in its reaction to virus X and, although not immune, has very high resistance.

It is not disputed that, with a realization of the danger of virus X, a breeder could launch a new variety while it is still free, and that, with the modern concern over varietal impurities in seed stocks, the variety could remain free for some time with little difficulty. But without precautions, it is well known that a new variety exposed to contamination under modern conditions becomes infected rapidly. It is on record that 'Up-to-Date' was mixed at an early age with other varieties, among them 'Magnum Bonum'; had infection been prevalent at that time, the variety would surely have acquired it, and its seeming freedom for many years argues that virus X had not properly established itself in Britain when the century opened.

'Up-to-Date' cannot be considered without reference to what happened before or occurred afterwards, and one must also consider the evidence about older and younger varieties.

If what has been written is correct, 'Up-to-Date' and its contemporaries must have been the first varieties in Britain to succumb to virus X. But varieties degenerated from obscure causes long before 'Up-to-Date'. Leaf-roll and virus Y must have destroyed many varieties in the past, but their symptoms cannot usually be classed as obscure, although there are some varieties which react in a fairly mild way. A much more likely cause of an obscure decline is virus A. In the absence of virus X, it produces symptoms which are not very conspicuous; and it seems able to spread rapidly even in places like Donegal (Clinch *et al.* 1938) or northern Maine (Schultz, Bonde & Raleigh, 1934) where the other aphis-borne viruses are rare or virtually absent.

'Champion' is the only old variety about which there is enough evidence to merit discussion. Introduced in 1876, it became so popular that for twenty years it occupied 75% of the total acreage under potatoes in Ireland, but towards the end of the century it began to deteriorate, and eventually became almost wholly infected with 'mosaic' (Davidson, 1928). The actual viruses were not determined at the time, but in 1935 Clinch *et al.* (1938) examined a stock which was supposed to represent some of the old degenerate 'Champion'. They found it to be completely infected with virus A but there was only 4% infection with virus X. It would be unwise to base too much on this single result, but the fact remains that in the one instance[1] in which an apparently typical case of degeneration in an old variety has been investigated, it was virus A and not virus X which was responsible. There is another piece of evidence which supports this. Both Davidson (1928) and Clinch *et al.* (1938) comment that the leaflets of the degenerate 'Champion' were reduced in size; reduction in size is a symptom of virus A but not of ordinary strains of virus X. If virus X was present in the degenerate 'Champion', it must have been in a complex which also contained virus A. But there is no evidence of a complex, and, as Clinch, Loughnane & Murphy's results show, the symptoms could have been produced by virus A alone.

'Magnum Bonum', said to have been very susceptible to mosaic (Salaman, 1926), may also have been a victim to virus A.

Of equal importance to our discussion are the modern varieties, of which 'Kerr's Pink' and 'Majestic' may be taken as examples. 'Kerr's Pink' was introduced under its present name in 1917, and 'Majestic' in 1911. Both became very popular in the 1920's and, though they have had to give way a little to new competitors like 'Arran Banner', there is no evidence that they have since weakened to any marked extent. Both are heavily infected by virus X, and it will be asked why, if this is so, they have not deteriorated as 'Up-to-Date' deteriorated. The answer is that they must have deteriorated, if one accepts the modern evidence about the effect of virus *X* on yield, but that the deterioration probably took place before they achieved nation-wide popularity, and thus escaped notice. That they were heavily infected by virus *X* before they became popular is no mere surmise, but is evident from the tests made in Britain with these varieties at an early date. It would, therefore, be unfair to contrast the careers of 'Kerr's Pink' and 'Majestic' with that of 'Up-to-Date'. If they have never had the pre-eminence which 'Up-to-Date' held in its hey-day, one can at least say that they never had the long spell free from disease which 'Up-to-Date' enjoyed; and we shall not know how they compare in intrinsic merit until seed of 'Kerr's Pink' and 'Majestic', free from virus *X*, is planted on an extensive scale.

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[1] The evidence is that in North America virus X came earlier than in Europe, and North American contemporaries of 'Champion', like 'Green Mountain', were completely overrun by the time they were examined. Virus X was found in time for clues to its history to be left in European varieties, but not in North American.

A disability similar to that of 'Kerr's Pink' and 'Majestic' is probably common among modern susceptible maincrop varieties, many of which have never had a proper chance to do their best.

CHANGES IN THE ABUNDANCE AND LONGEVITY OF VARIETIES; THE CONSEQUENCES OF THE MODERN SEED INDUSTRY

The great difference in health between the potatoes of Basutoland and Tristan da Cunha and modern varieties is a reflexion of the changes which have come over the potato industry in the last 100 or 150 years. It is not just a matter of chance that virus *X* has, it seems, only recently become troublesome: conditions now favour the disease and give it every chance to spread, whereas in earlier times circumstances were against the virus and would have made it innocuous even if it was present, which is doubtful.

One of the most significant changes during the last 100 years is the dependence of the industry now on a small number of varieties most of which are fairly old. In Scotland, 'Kerr's Pink' and 'Majestic' made up nearly half the acreage in 1937 and probably considerably more than half the total yield. With the varieties 'King Edward', 'Epicure', 'Golden Wonder' and 'Great Scott', over three-quarters of the total acreage was accounted for. Of these six varieties, 'Kerr's Pink', introduced in 1917, is the youngest. With local variations the story is much the same elsewhere as in Britain. In South Africa, 'Up-to-Date' and 'Arran Chief', with an average age of forty-five years, still dominate the fields. In the United States, 63 % of the total acreage of seed certified in 1941 was planted with 'Irish Cobbler', 'Triumph' and 'Green Mountain', all of which date well back to the last century. The only young variety of any consequence in 1941 was 'Katahdin', though since that time the new breeding efforts by the Department of Agriculture and others have somewhat changed the position: 'Katahdin' has gone ahead, and several new varieties like 'Sebago' have shown their worth.

For contrast, consider the position in Britain early in the nineteenth century. Potatoes had only recently been cultivated as a field crop, and far into the century continued, except in Ireland, to play only a small part in a system of farming still given over to the three old staples: corn, cattle and sheep. Little advance had been made in breeding; varieties were numerous, mostly of local importance only, quickly bred and quickly discarded, and often of poor quality. The raising of seedlings was common practice—agricultural manuals told how to do this—and seedling varieties seem to have served fairly well as maincrops or lates. Earlies were possibly more restricted, but many of the names—'Foxe's Seedlings', 'Mather's Seedlings', 'Smith's Seedlings', to quote a few from Dickson's *Practical Agriculture*, published in 1805—smack of hasty breeding and hasty launching. How long this state of affairs continued is not known. The industry became better organized as the years went by, but even in 1835 when Loudon published his *Encyclopaedia of Gardening*, or 1836 when Lawson published his *Agriculturalist's Manual*, varieties were still (to quote Loudon) 'innumerable...and continually undergoing change. In general, every town and district has its peculiar and favourite varieties, early as well as late.' There were no standards of tuber-shape or colour, and varieties were so bewilderingly abundant that purchasers of seed were advised by Loudon to give a general description of the size, colour, form and quality wanted, and whether for an early or a late crop. If conditions were unstable in 1836, they became very much more unsettled ten years later, when blight arrived, destroyed most of the old varieties, and, in forcing a search for resistant types, introduced a spell of quick varietal change that lasted for another twenty or thirty years.

As Salaman (1931) puts it, 'the stimulus to the production of new varieties prior to 1848, over and above man's native itch to produce "better varieties", was undoubtedly the deterioration, or as the term then was, the degeneration, of varieties. This degeneration, we now know, was the sequel of infection by virus disease, and at times during the 100 years prior to 1830 it threatened the very existence of the potato in England.' There was at that time nothing of the nature of the modern seed industry. It is true that John Holt, as early as 1790, recognized the value of seed from Scotland, but the dependence of the English potato industry on Scottish or Irish seed was a long way off. Apart from the lack of technical knowledge and the low state of organization of the industry generally, transport alone was a major difficulty. Admittedly, there were canals—their spread in England was more or less contemporaneous with the establishment of potatoes as a field crop—and main roads were improving; but neither the Turnpike Trustees nor the parish authorities gave much attention to the secondary roads which were often in a poor state during those months when seed potatoes must be shifted, and railways were not of much importance until the 'forties in England and later elsewhere. Local resources were more in evidence and a change of varieties was the ultimate counter to the curl.

The absence of a regular outside source of seed and the perpetual change of varieties must have been powerful influences in keeping virus *X* down, if the virus occurred at all. Nowadays, one gets new seed from the seed industry, with a fair guarantee of freedom from dangerous proportions of leaf-roll or severe mosaic, but with no suggestion that susceptible varieties are free from virus *X*. Modern practices control leaf-roll and severe mosaic, but virus *X* has no real check and can accumulate throughout the whole life of the variety. But 100 to 150 years ago, new stocks, raised from seed, or new varieties were free from all viruses, and there was no control of leaf-roll or severe mosaic by new seedling varieties without the simultaneous control of virus *X*. General experience shows that virus *X* spreads relatively slowly and only by contact (of foliage or roots, or of the shoots of sprouted tubers), which precludes mass infection of fields of new stocks by those of old, as commonly happens with the aphis-borne viruses. The ceaseless change of varieties, which was going on in Scotland and Ireland as well as in England, in what are now good seed areas as well as in what are now ware-producing districts, cannot have failed to make conditions most adverse to virus *X*.

Other conditions contributed to the result. The whole story of the potato, from the time it came to Europe until quite recently, has been one of circumstances unfavourable to a slow-spreading virus transmitted by contact, and is worth briefly considering in this light.

A TENTATIVE OUTLINE OF THE HISTORY OF POTATO VIRUS X IN THE DOMESTIC POTATO

One may conveniently divide the history of the potato outside its ancient home in South America into three periods, and discuss them with particular reference to Britain, where the sequence of events was much the same as elsewhere.

The earliest period had three characteristics pertinent to our inquiry. First, potatoes were commonly grown from true seed, and a change of varieties was even more frequent than it was later; the bearing of the repeated raising of new seedlings on our problem has just been discussed. Secondly, potatoes were grown sparsely as a garden crop which was more a luxury or a curiosity than anything else. Thirdly, potatoes were commonly allowed to grow as volunteers from tubers left behind in the ground when the previous crop was lifted. This procedure had the backing of Evelyn, who in 1699 advised: 'Plant potatoes in your worst ground. Take them up in November for winter spending; there will enough remain for stock, though ever so exactly gathered.' Evelyn's opinion seems to have been fairly general;[1] and it is stated as a well-ascertained fact in the *General Report of Scotland* (vol. II, p. 111), also quoted in Loudon's *Encyclopaedia of Gardening* (1835), that in the year 1725–26 the few potato plants then existing in the gardens about Edinburgh were left in the same spot of ground from year to year, a few tubers perhaps being lifted in the autumn and the rest covered with litter against the winter's frost. To appreciate the effect of the last two characteristics of potato culture at that time, one must accept the evidence of Loughnane & Murphy (1938), of unpublished work in South Africa, and of Roberts (1946) in England that virus X spreads only by the direct contact of healthy and infected plants. On this evidence, the virus causes a social disease, only able to spread when plants touch one another, and checked if planting is sparse. Equally adverse to the spread of infection is the growth of plants as volunteers from unharvested tubers, because the consequent tendency is to keep members of a clone together and thus to keep inherited disease within the clone, with little chance of spreading except where clones overlap.

This early phase continued for about two centuries in most of Western Europe, except in Ireland where progress was quicker. While it lasted, conditions were probably so unfavourable to virus X that even if it had come in with the two original introductions of the potato, it is likely to have died out; while other introductions—if there were unrecorded introductions at this time—would have been cared for in the same way.

For about another century potatoes were grown as a field crop on an ever-increasing scale, and there was now that close contact between plants in a row and that mixing of members of different clones which are necessary for virus X to spread. But there was still a very frequent change of countless varieties, first under the stress of curl and as an attempt to develop better types, and later, after 1845, in the effort to overcome blight; and conditions in this respect remained unfavourable to virus X. In particular, the purge of varieties which followed the advent of blight would have had a potent effect in any slow-spreading inherited virus if one chanced to have been present.

It is of this second phase, some time before the arrival of blight, that the potatoes of Basutoland and perhaps those of Tristan da Cunha are relics.

The third phase began about seventy or eighty years ago, when conditions changed abruptly, and the industry entered a period of stability. In England and Scotland, 'Magnum Bonum', 'Up-to-Date', and practically as contemporaries, 'King Edward', 'Kerr's Pink' and 'Majestic' bridged in three spans a gap of seventy years; while in Ireland, 'Champion', and in North America, varieties like 'Green Mountain' and 'Triumph' had even more spectacular careers. The great breeders introduced varieties that were grown nation-wide for very many years, and their superb achievements provided the stability that, ironically enough, gave virus X the conditions it needs. The one-sided concentration of the seed industry on leaf-roll and severe mosaic failed to provide an adequate check; and it is during this period, it is believed, that virus X for the first time achieved menacing ubiquity in the domestic potato.

North America was probably affected before Britain. So far as I am aware, no virus-free tubers have ever been found in the old standard North American varieties, except for a single tuber of 'Early Rose' found by Burnett & Jones (1931), whereas stocks free from virus X are available in every British variety in which they have been sought. It is true that in one instance, that of 'Up-to-Date', virus-free stocks had to be found in Australia or South Africa; but then it should be remarked that attempts to find virus-free tubers of varieties of American origin have been as unsuccessful in Australia as they have been in America. If on the evidence of 'Up-to-Date' we choose the early part of this century as the time when virus X became widespread in Britain, we may perhaps allow that it was common in North America towards the end of last century.

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[1] Evidence is accumulating that the original European potatoes were short-day types from the Andes; and the difficulty mentioned by Evelyn of harvesting the crop was probably the consequence of the stimulus to the development of stolons which the long European summer day gives to short-day Andean varieties. Seemingly, this character had not been lost by Evelyn's day. Similar profuse development of stolons occurs with some of the Basuto varieties, although these belong to a later period, and nothing short of putting the soil through a sieve is likely to recover the whole crop.

It is possible, but unlikely, that virus X was present in the domestic potato, but was a rarity kept under control by adverse circumstances which persisted until the last seventy years or so. More probably, it came into the United States with Central or South American potatoes, like those sent by the United States consul at Panama to Goodrich in 1851, and took very many years to multiply to the point of commonness, first in North America and then generally. South America was most likely to have been the home of the virus, partly because of the age of the potato industry and partly because some varieties there have apparently existed for a very long time and give that continuity in which the virus can thrive; and Salaman (1939) has already drawn attention to the significance of the high amount of infection in potatoes from the region of Lake Titicaca. In the absence of adequate information, however, it is unprofitable to pursue this aspect of the question any further.

DISCUSSION

There seems little doubt that the modern potato seed industry has muddled its business and given us virus X as a needless major problem. This discussion on the history of the virus and other topics was written primarily with the object of peeling away the irrelevancies and leaving this hard kernel of unpalatable fact. Virus X spreads slowly in a field, and, seemingly, can easily be prevented from entering from without; with these limitations nothing short of very poor organization would have allowed the virus to get the hold it has. That the mistakes have been made unwittingly is rather beside the point. Lack of knowledge may explain how the organization developed in the past, and allowed the seed industry to concentrate on controlling leaf-roll and severe mosaic[1] while distributing infected stocks which took virus X wherever they went. But it will not excuse its continuation in the future.

It is not desired to discuss at length the losses which have been observed from virus X. From the work of Scott (1941) in Scotland, Bald (1943, 1944*b*) in Australia, Schultz & Bonde (1944) in Maine, and Smith & Markham (1945) in England it appears that losses in yield of about 10% may be expected even from the weakest strains of the virus, while ordinary strains cause losses of about 20% or more. A few varieties are immune and a few are still only slightly infected, but taken all in all national losses can probably be conservatively estimated at 10% of the potato crop. On the pre-war census of potato production, this meant a world loss of some 800,000,000 bushels yearly from the virus, all through bad seed. To look at the matter in another way, to cause a loss of 10–20% the proportion of leaf-roll or severe mosaic must be high; healthy plants compensate largely for the losses in yield of their immediate neighbours with leaf-roll and severe mosaic; and for losses to be severe the proportion of infection must be high—probably higher than good farmers will tolerate. In short, good farmers, careful of their seed, are probably losing more from virus X than from the leaf-roll and severe mosaic viruses. Yet the seed industry continues to have strict regulations about leaf-roll and severe mosaic, but permits virus X to be present in unrestricted amounts, only limiting the severity of the strain in the better grades of seed.

Clearly, there is an urgent need for a change. This has been realized for some time—ever since Eire took the lead in growing virus-free potatoes, as Murphy (1938) has described—and it will probably not be long before seed free from virus X is on the market. What it is wished to stress here is that freedom from virus X is an elementary requirement for good seed, and that seed free from virus X should be available, not as something special at fancy prices, but as the ordinary article, as it was in previous centuries.

[1] Severe mosaic is used in the British sense of the term and includes what is called mild mosaic in America (i.e. crinkle).

On wider issues, current practices give cause for anxiety. That a few modern varieties have replaced the 'innumerable' varieties of 100 years ago is not a feature peculiar to the potato industry. It has been said that a century ago a large apple orchard was likely to contain more varieties than are now grown on commercial scale in the whole of England. In the United States, South Africa and many other countries the orange industry is, and has been for a long time, dominated by two varieties. And so the story proceeds for crop after crop. Diversity and abundance of varieties have given way to standardization and dependence on a few favoured sorts. With crops grown from seed, this is dangerous enough. With crops reproduced vegetatively, the risk is much greater; and what happened with virus *X* in potatoes may happen, or may have happened, in other crops (or even, for all we can tell, with other viruses, still undetected, in the potato, as Ross's (1946) evidence for another latent virus in some strains of 'Green Mountain' reminds us). We may try to assure ourselves that potato virus *X* was an exception, a passing difficulty which was revealed and is now being met. But we have no real grounds for this assurance. In potato virus *X* we have a problem which in respect of the availability of convenient indicator plants—tobacco, *Datura*, *Capsicum* and potato varieties which react with a top necrosis—is unusually favourable for investigation and discovery. For viruses in other crops, like Citrus, apples and the rest, one can call to mind no likely array of indicators of such merit, and must admit that, if standardization and the reduction in number and renewal rate of varieties has had the same effect in promoting the development of latent viruses in other crops as in the potato, our chances of detecting these viruses at present are not very great. From the history of potato virus *X* we may take warning of the danger of modern practices.

SUMMARY

Although virus *X* is carried by the potato almost without symptoms and was first discovered only twenty-two years ago when it was already nearly ubiquitous, its history outside South America can be traced over the centuries with some assurance of accuracy. Potatoes of diverse varieties were brought to Basutoland and Tristan da Cunha in the last century and since grown in isolation. They are free from virus *X* which, because the virus is not thrown off by clones which have become infected, indicates a high general level of health at that time. The change which has come about elsewhere since then is not merely fortuitous. A hundred years ago varieties were innumerable and mostly short-lived; and between changes of variety there was normally little chance for the virus to accumulate. Nowadays the varieties which are extensively cultivated are relatively few and mostly long-lived. With their longevity has come the chance for the virus to accumulate; and the accumulation has been helped by a seed industry which controls leaf-roll and severe mosaic, thus obviating the need for changing varieties, but not virus *X* except in its more severe strains. American varieties were apparently infected early: too early for the history of the attack to be traced. British varieties seem to have been attacked later, and the evidence of 'Up-to-Date', with a hint of confirmation from 'Champion', is that infection was scarce until about the second decade of this century.

Losses from virus *X*, conservatively put at 800,000,000 bushels a year for the world over, are both an indictment of the organization of the seed industry and a warning against the danger of abandoning varietal abundance and novelty in crops which are propagated by vegetative means.

ADDENDUM

Although the evidence is strong that virus *X* became widespread in the European potato only fairly recently, it is not so satisfactory about the actual date of considerable spread. Mainly on the evidence of 'Up-to-Date', the second decade of this century was suggested for potatoes in Britain. Further evidence has now been seen which confirms this, and indicates that the virus was uncommon during the first decade.

The potato variety 'Northern Star' was introduced by Findlay in Britain in 1900, had a brief boom, and then faded out as a commercial variety. Some time fairly early in its history, most likely during its brief spell of popularity in Britain, it went to Kenya and became accepted there as a 'native' potato under the names Kinongo and Kerai. Like the varieties of Basutoland and Tristan da Cunha, 'Northern Star' in Kenya is a relic of the past, but of a more recent past which can be fairly accurately dated. Like the other varieties, it went into isolation before becoming infected, to an appreciable extent at any rate, by virus *X*; for Nattrass (Report of the Senior Plant Pathologist, *Kenya Dep. Agric. Rep. for* 1945, p. 90) examined samples from native shambas and found them free from the virus.

So general is the belief in the antiquity and ubiquity of potato virus *X* that Nattrass could not bring himself to believe that the samples were free because the original importations were free. He suggests that true seed may have been set from time to time and virus-free seedlings raised which do not differ essentially from the parent variety. But we can exclude this suggestion at once, because 'Northern Star' has no pollen.

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NOTE ADDED IN PROOF

Very recently, Clinch & McKay (*Rev. Appl. Mycol.* **26**, 413, 1947) stated that their results gave no evidence of a reduction of yield by mild strains of potato virus *X*. This difference from the results of others may be more apparent than real. Bald emphasized that in Australia virus *X* does not reduce the yield until tuber formation is far advanced; while Clinch & McKay's results were mainly with 'Up-to-Date' potatoes prematurely killed by blight in August.

The Coritanian Elm. By R. Melville

(With 5 Text-figures)

[Read 8 May 1947]

It has been the custom in the past to include all the smooth-leaved elms of Britain under the one species now known as *Ulmus carpinifolia* Gleditsch. The leaf form and pattern of variation in this species were studied in a recent paper (Melville, *Journ. Linn. Soc., Bot.* LIII, 83, 1946), and it is clear that there are many British forms that do not fall within its range. Some of these forms constitute another species, which is not at present known with certainty from the Continent. On the other hand, *U. carpinifolia* is widespread in Europe and its status as a British citizen still doubtful.

The new species first came under my notice when searching for Horwood's *U. elegantissima* in the neighbourhood of Leicester in 1936. Some material of it shown to Horwood was repudiated as distinct from his elm, which on later investigation proved to be a hybrid between the Wych elm, *U. glabra* Huds. and the Plot elm, *U. plotii* Druce (Melville, *Proc. Linn. Soc.* CLI, 159, 1939). The area explored at that time was part of the territory formerly occupied by an ancient British tribe, the Coritanae, and it therefore seemed appropriate to name the new species *U. coritana.*

In the intervening years the range of variation within the species has been studied and its distribution mapped out. Material in the national and other herbaria has been examined and specimens have been found under various names. Apart from misidentifications, the only names that need be considered are *U. nitens* Moench. var. *sowerbyi* Moss and *U. nitens* var. *hunnybunii* Moss, published in the *Cambridge British Flora* (II, 90, 1914). Much of the material in herbaria under var. *sowerbyi* belongs to *U. coritana* and for a time it seemed that this varietal name could be adopted for the species. The tree from which Moss' type material was gathered is situated in Christ's Pieces, Cambridge. I have examined both the tree and several herbarium specimens taken from it at different times. With a fuller knowledge of *U. coritana* it now seems highly probable that *U. nitens* var. *sowerbyi* Moss is a hybrid. Moss' name cannot therefore be used. The figure of *U. glabra* in *English Botany* (t. 2248), to which he refers, represents a different elm. Moreover, as pointed out earlier (Melville, *Journ. Linn. Soc., Bot.* LIII, 86, 1946), there is some confusion concerning the figure and the specimens on which it is reputed to have been based. Quite apart from this, the name *U. glabra* Smith is not available as it is antedated by *U. glabra* Huds. The reference to *U. tortuosa* Host must be excluded, as apparently authentic specimens of this continental elm, at Kew, differ markedly from *U. coritana.* Moss' other variety, *hunnybunii*, may also be a hybrid of *U. coritana*, but it requires further study. It lies outside the pattern of variation described in this paper.

The rather spreading open crown of *U. coritana* does not at once distinguish it from other elm species and hybrids. The leaves are of a bright and pleasing shade of green, and coriaceous in texture, and their marked asymmetry and characteristic shapes contrast sharply with those of other smooth-leaved elms. The blunt and often complex serrature provides other points of difference. In the detailed descriptions below, the rectangular co-ordinates used to define the mean leaf shapes were obtained by a method previously described (Melville, *Ann. Bot., Lond.*, N.S. I, 673, 1937). The measurements are given in order from the base of the lamina to the tip and the breadths and petiolar ratios are expressed as percentages of the lamina length.

Ulmus coritana Melville, sp.nov. Arbor usque 20 m. alta, ramis patulo-adscendentibus, ramulis glabris spadiceis. Folia ± coriacea, laete viridia, supra glabra, infra pallidiora fasciculis pilorum in nervorum axillis conspicuis et glandulis numerosis munita, anguste usque late ovata acuta, basi valde inaequali, latere longiore basi lobo rotundato vel arcuatim ad petiolum juncto, marginibus dupliciter serratis, serraturis 2–4 obtusis, nervis lateralibus 8–12.

A rather spreading tree, up to 20 m. high, with ascending branches and rather open crown. First-year branchlets of the short roots 1–2 mm. diameter, smooth, chestnut brown, with scattered inconspicuous lenticels. Short shoots with 3–5 leaves; distal and subdistal leaves coriaceous, bright green, glabrous and shining above, paler below, glabrous except for conspicuous axillary tufts and numerous glands; narrowly to broadly ovate, acute, base usually strongly asymmetrical, lower part of the midrib often curved towards the short side, long side meeting the petiole in a rounded lobe or sometimes at an angle; margin biserrate, serration at one-third lamina length from the apex, rather blunt, distal edge concave, often with a subsidiary tooth, proximal edge with usually 3 or 4 subsidiary teeth, the third from the tip larger than the others and supplied by a rather prominent curved secondary nerve from near the tip of the main lateral nerve; petiole 2–15 mm. long, pubescent above, glabrous below. Number of main lateral nerves on long side 8–12. Lamina length of distal and subdistal leaves 3–9 cm. Stipules caducous. Vegetative buds 2–4 mm. long, ovate, acute, bud scales 4–5, imbricate, shortly fringed.

var. **media** Melville, var.nov. Folia distalia et subdistalia ramulorum brevium late ovata, acuta, 3·5–7 cm. longa, latere breviore fere semiorbiculata, latere longiore basi lobo rotundato 3–9 mm. infra latus brevius ad petiolum juncto, petiolo 4–10 mm. longo.
Typus in Herb. Kew., Melville no. 38.79.

Distal and subdistal leaves of the short shoots broadly ovate acute, lamina 3·5–7 cm. long, strongly asymmetrical, short side nearly semicircular, long side meeting the petiole in a rounded lobe or curve 3–9 mm. below the short side; number of main lateral nerves on long side 8–12; petiole 4–10 mm. long.

The type variety: type in Herb. Kew., Melville no. 38.79; young tree, 20 ft. high, in a copse two miles north of Lutterworth, Leicestershire, 7. viii. 1938. Foliage and mean leaf shapes shown in Fig. 1 B–F. Habit sketch (Fig. 1 A) from Melville no. 46.31, a 50 ft. tree in a roadside hedgerow, ¼ mile west of Ermine Street, on the Tadlow road, Cambridgeshire.

Co-ordinates for the mean leaf shapes of the Lutterworth tree no. 38.79.

Distal leaves of short shoots:

Short side: 14/0, 20/14, 30/25, 40/30, 50/32, 60/30, 70/26, 80/17, 90/6·8.
Long side: 2·9/0, 0/5·1, 10/15, 20/25, 30/31, 40/33, 50/33, 60/30, 70/26, 80/17, 90/7·4.
Petiolar ratio 13; mean length of lamina 6·6 cm.; mean no. of lateral nerves, long side, 11.

Subdistal leaves of short shoots:

Short side: 16/0, 20/16, 30/26, 40/31, 50/32, 60/30, 70/25, 80/18, 90/7·9.
Long side: 4·0/0, 0/6·6, 10/19, 20/29, 30/33, 40/34, 50/33, 60/30, 70/25, 80/17, 90/8·1.
Petiolar ratio 15; mean length of lamina 6·0 cm.; mean no. of lateral nerves, long side, 11.

var. **angustifolia** Melville, var.nov. Folia distalia et subdistalia ramulorum brevium anguste-ovata usque ovato-lanceolata, acuta, valde asymmetrica, lamina 4–9 cm. longa, latere longiore 3–15 mm. infra latus brevius ad petiolum arcuatim juncta, petiolo 7–15 mm. longo.
Typus in Herb. Kew., Melville no. 38.142.

var. *angustifolia* Melville. Distal and subdistal leaves of the short shoots narrowly ovate to ovate-lanceolate, lamina 4–9 cm. long, strongly asymmetrical, the long side meeting the petiole in a rounded curve 3–15 mm. below the short side, number of main lateral nerves on long side 8–12, petiole 7–15 mm. long.

Varietal type in Herb. Kew., Melville no. 38.142, 50 ft. tree by roadside pond north of Stowupland, East Suffolk, 4. ix. 1938. Short shoot and mean leaf shapes shown in Fig. 2 A, B, G, H.

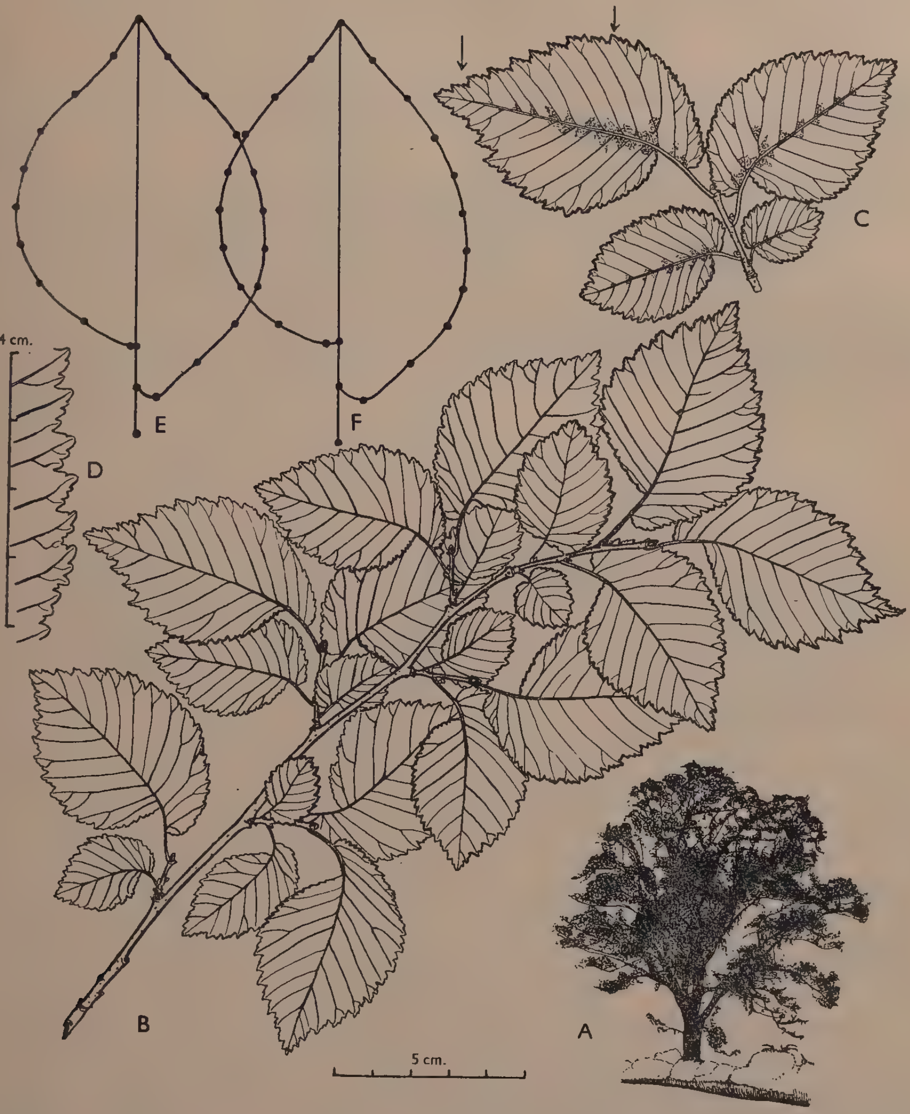

Fig. 1. *Ulmus coritana* var. *media* Melville. A, habit sketch of a tree in Cambridgeshire, Melville no. 46.31; B, spray of foliage; C, single short shoot, lower surface, showing axillary tufts; D, enlargement of marked portion of margin of distal leaf of C; E and F, mean leaf shapes, E of distal, F of subdistal leaves of short shoots. B–F from the type tree, Melville no. 38.79, near Lutterworth, Leicestershire.

Co-ordinates for mean leaf shape of the Stowupland tree no. 38.142.
Distal leaves of short shoots:

Short side: 6·6/0, 10/4·1, 20/12, 30/18, 40/22, 50/23, 60/22, 70/19, 80/13, 90/5·8.
Long side: 1·7/0, 0/3·9, 10/15, 20/19, 30/22, 40/24, 50/23, 60/22, 70/18, 80/12, 90/5·0.
Petiolar ratio 15; mean length of lamina 5·1 cm.; mean no. of lateral nerves, long side, 10.

Subdistal leaves of short shoots:

Short side: 8·7/0, 10/1·9, 20/10, 30/17, 40/21, 50/23, 60/22, 70/19, 80/13, 90/5·1.
Long side: 2·1/0, 0/4·2, 10/15, 20/19, 30/22, 40/23, 50/24, 60/22, 70/18, 80/13, 90/4·9.
Petiolar ratio 20; mean length of lamina 6·3 cm.; mean no. of lateral nerves, long side, 10.

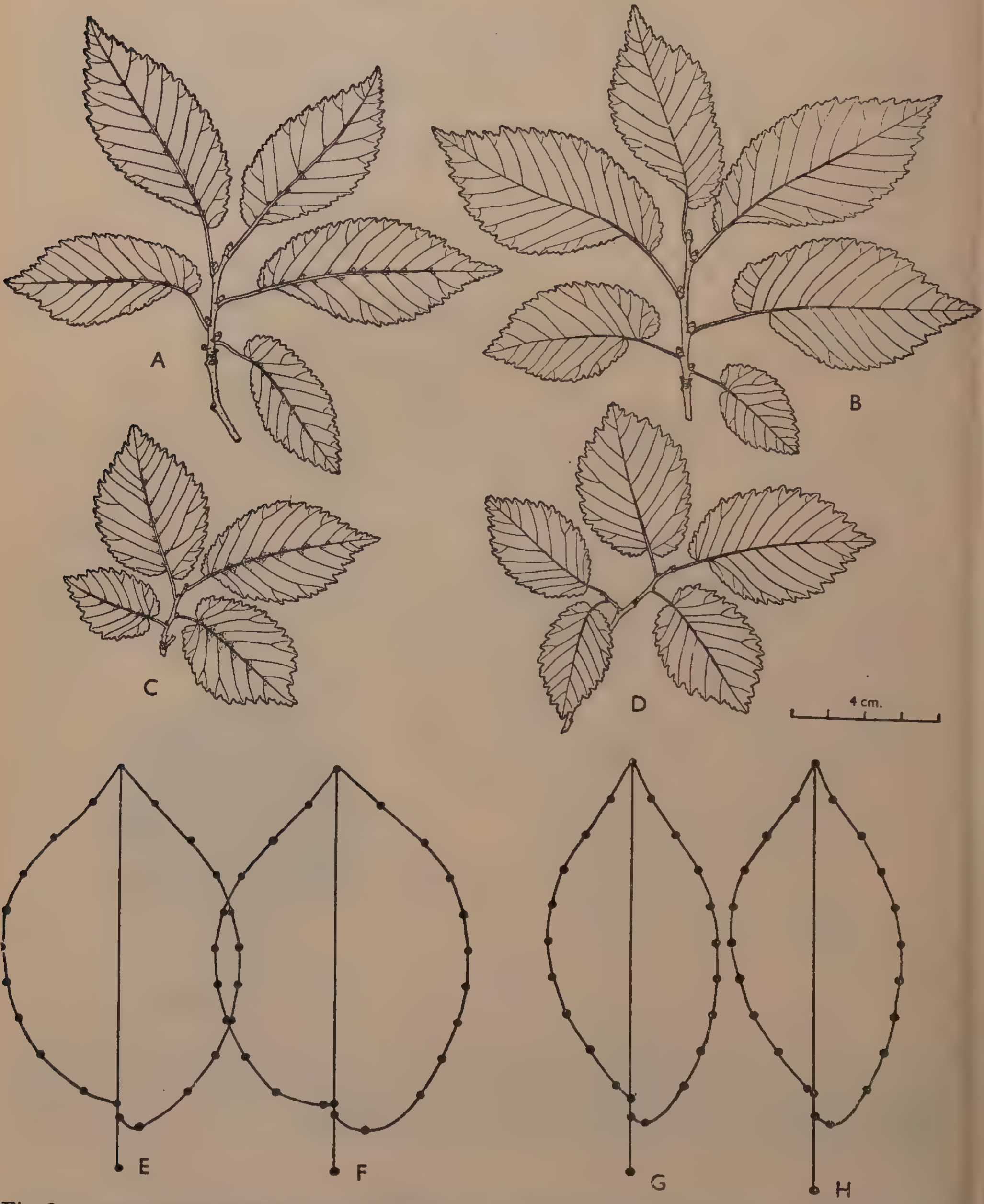

Fig. 2. *Ulmus coritana* Melville. A, B, G and H, var. *angustifolia* Melville from the type tree Melville no. 38.142, Stowupland, East Suffolk. A, lower, and B, upper surface of typical short shoots; G and H, mean leaf shapes of G, distal, and H subdistal leaves of short shoots. C, D, E and F, var. *rotundifolia* Melville, from the type tree, Melville no. 39.35, near Winslow, Bucks. C, lower, and D, upper surface of typical short shoots; E and F, mean leaf shapes of E distal, F subdistal leaves of short shoots.

var. **rotundifolia** Melville, var.nov. Folia distalia et subdistalia ramulorum brevium late-ovata, acuta, asymmetrica, lamina 2·5–5·5 cm. longa, latere longiore basi lobo rotundato 1–3 mm. infra latus brevius and petiolum juncto, petiolo 2–9 mm. longo.

Typus in Herb. Kew., Melville no. 39.35.

var. *rotundifolia* Melville. Distal and subdistal leaves of the short shoots broadly ovate acute, lamina 2·5–5·5 cm. long, the long side meeting the petiole in a rounded lobe 1–3 mm. below the short side, number of main lateral nerves on the long side 8–12, petiole 2–9 mm. long.

Varietal type in Herb. Kew., Melville no. 39.35, 35 ft. tree in roadside hedge, two miles south-east of Winslow on the Aylesbury Road, Bucks., 18. vi. 1939. Short shoot and mean leaf shapes shown in Fig. 2 C, D, E, F.

Co-ordinates for mean leaf shapes of the Winslow tree no. 39.35.

Distal leaves of short shoots:

Short side: 6·6/0, 6·5/0·9, 10/10, 20/22, 30/28, 40/31, 50/33. 60/31, 70/27, 80/19, 90/7·7.
Long side: 2·8/0, 0/5·6, 10/19, 20/27, 30/31, 40/33, 50/33, 60/31, 70/27, 80/20, 90/9·2.
Petiolar ratio 15; mean length of lamina 4·1 cm.; mean no. of lateral nerves, long side, 10.

Subdistal leaves of short shoots:

Short side: 7·2/0, 6·7/3·5, 10/16, 20/25, 30/30, 40/33, 50/34, 60/31, 70/26, 80/18, 90/7·9.
Long side: 4·3/0, 0/8·2, 10/24, 20/30, 30/34, 40/36, 50/37, 60/35, 70/31, 80/24, 90/12.
Petiolar ratio 16; mean length of lamina 3·7 cm.; mean no. of lateral nerves, long side, 9.

The three varieties described above are connected by intermediate forms. Round-leaved individuals, falling within the limits of var. *rotundifolia*, are the least common and have been found only in the southern parts of the territory occupied by the species. Intermediate and narrow-leaved individuals are much more abundant and widespread, but var. *angustifolia* is most common in the north of the territory and is absent from the south. The change in the population is gradual and is best described as a topocline in decreasing breadth and increasing asymmetry of the leaves from south to north. Leaf size also increases slightly in the same direction along the cline.

The validity of defining varieties in a population in which continuous variation exists is open to question. The two ends of the series are strikingly different and in the absence of intermediates one would have no compunction in describing the terminal members as varieties or even species. In order to describe the species adequately, it appears equally necessary to define the central portion of the series as a third variety. If one accepts Du Rietz's definition of a variety as 'a population of one or several biotypes forming a more or less distinct local facies of a species', it can be claimed that the varieties here described represent local facies of the species, though somewhat ill-defined facies on account of the overlap of the varietal territories.

The mean leaf forms shown in the diagram are slightly idealized as the curvature of the base of the midrib, which is usual in vars. *media* and *angustifolia*, is not shown. In making the measurements, the breadth of the lamina at this part of the leaf was taken at right angles to the midrib. This procedure is the cause of the slight inflexion of the outline near the base of the long side. The margin in living plants normally forms a rounded curve in this region, but a similar inflexion sometimes occurs, especially if the midrib has remained straight, instead of being pushed out of alignment by the unilateral growth of the leaf base.

The principal difference between the varieties *media* and *angustifolia* is one of leaf breadth. It is possible to calculate from the mean leaf shape of one variety a series of leaf shapes forming an arithmetical series differing only in breadth. This has been done, using as the starting-point the mean shape of the subdistal leaves of short shoots of the type of var. *media* (Fig. 3). Taking this type as 100 %, the type of var. *angustifolia* falls between the 60 and 80 % members of the series. Individuals have been encountered in the field differing in leaf breadth from that of the 60 % member very nearly up to that of the 120 % member.

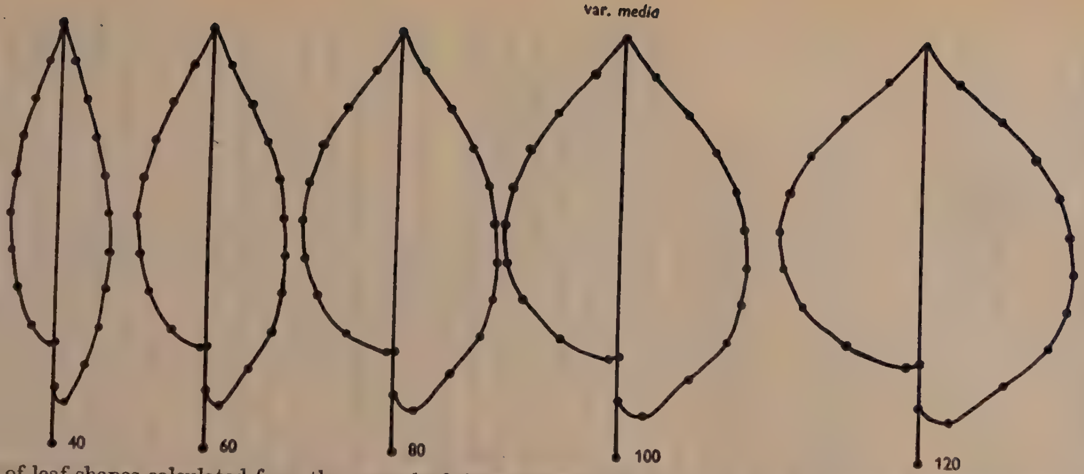

Fig. 3. A series of leaf shapes calculated from the mean leaf shape of subdistal leaves of *Ulmus coritana* var. *media* Melville (100) forming part of an arithmetical series differing only in breadth. The numerals indicate percentage breadths.

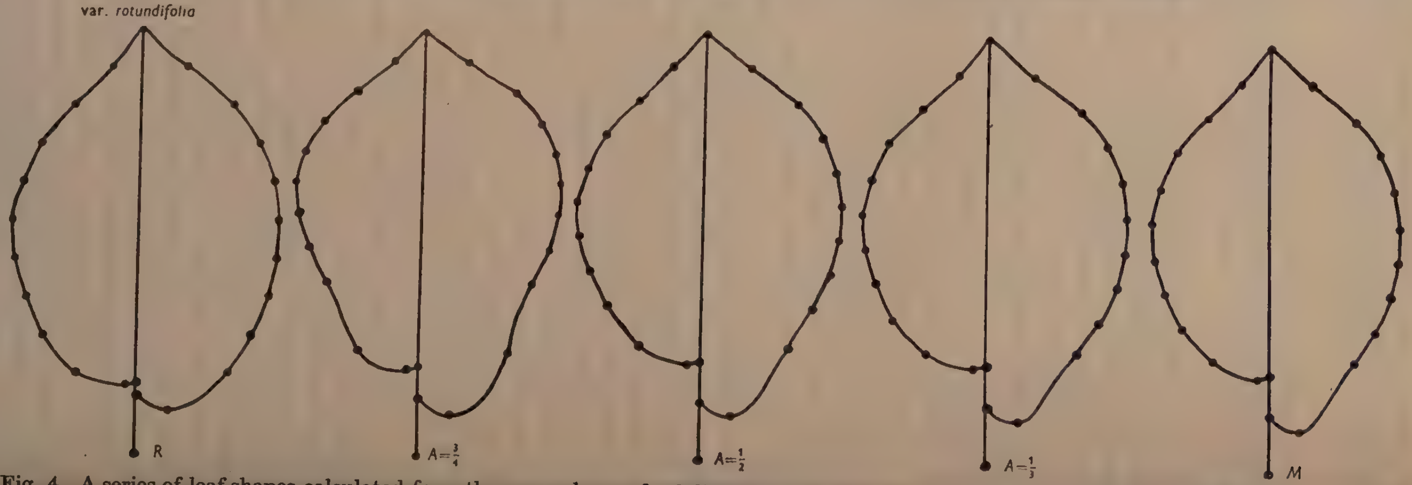

Fig. 4. A series of leaf shapes calculated from the mean shape of subdistal leaves of *Ulmus coritana* var. *rotundifolia* Melville (*R*), illustrating

Differences in leaf breadth are not the only kind of variation in shape encountered within the species. The type of var. *angustifolia* has a base rather less asymmetrical than that shown in this arithmetical series, while the type var. *rotundifolia* is very much less asymmetrical. The differences between the leaf shapes of var. *rotundifolia* and var. *media* could be accounted for by an increase in the rate of growth of the tissues of the leaf base on a round-leaved plant, resulting in a relatively greater growth in length of the basal region compared with that of the distal parts. Apart from modulations caused by differences in breadth, there is little difference in the form of the apical half of the leaves in *U. coritana*. Differences in asymmetry effect the basal half only. In order to produce such a result, it is clear that the effect of the growth factor concerned must decrease very rapidly from the base towards the apex. The petiole, also, shares in the increased growth rate, for on passing along the series, from the round-leaved to the narrow-leaved forms, it increases in length both absolutely and relatively to the length of the leaf.

An attempt was made to transform mathematically the mean shape of the subdistal leaves of var. *rotundifolia* into that of var. *media*. It was assumed that the factor governing growth decreased logarithmically from the base towards the apex and did not affect breadth. The factors required to modify the co-ordinates of length were calculated by applying the formula:

$$\log Fn = A^{n-1} \log F_1.$$

As the distance between the points of insertion of the long and short sides on the midrib in var. *rotundifolia* was 4% of the lamina length and 12% in var. *media*, the factor $F_1 = 3$. Units of 4% of the lamina length were then considered and different values of the modifying factor A were tried. The shapes obtained when the factor A is $\frac{3}{4}$, $\frac{1}{2}$ and $\frac{1}{3}$ are plotted in Fig. 4, all the longitudinal scales being reduced to the same total length for convenience of comparison. A very close approximation to the leaf shape of var. *media* was obtained when the factor A is $\frac{1}{3}$ and the similarity is enhanced if the breadth is reduced to the proportion obtaining in that variety: compare Fig. 4 *M* and Fig. 1 F.

The mathematical examination lends colour to the view that variation in leaf shape in *U. coritana* is primarily due to differential growth rates in different individuals. In the southern part of its range, changes in asymmetry seem to predominate, while in the north the more obvious variation is in breadth of leaf. Throughout the range, however, both types of variation are concerned in the observed modulations of leaf shape. The operation of a factor governing leaf asymmetry along the length of the leaf is a point of difference between *U. coritana* and *U. carpinifolia* that may be of primary importance in the differentiation of these species. In *U. carpinifolia* the observed alterations in asymmetry were brought about by lateral changes in the proportions of the leaf base (Melville, *Journ. Linn. Soc., Bot.*, LIII, 88, 1946).

It is perhaps remarkable that a cline in leaf shape should arise in a territory of about 100 miles in length, for this suggests that graded differences occur in climatic or edaphic factors of sufficient magnitude to affect the evolution of the species. The tree is found on a variety of soils, providing they are sufficiently moist, but no evidence is available at present to indicate that soil factors are responsible. As the cline runs from south to north there must be some gradation of climatic factors, but their importance is unknown. The species is almost confined to the valleys, for it rarely occurs above the 400 ft. contour.

The distribution, shown in Fig. 5, extends through East Anglia and across the Midlands, southward to the Thames valley and northwards to the Trent valley. In order to plot the three varieties, the ratio of length to breadth of subdistal leaves of short shoots was determined for all the available material. Arbitrary values were chosen as the limits of the varieties: below 1·5 for var. *rotundifolia*, 1·5–1·8 for var. *media* and above 1·8 for var. *angustifolia*. A number of individuals from Norfolk came in var. *media*, at but little below the limit set for var. *angustifolia*. More work is needed on the distribution, especially of the narrow-leaved forms in the north and of the western limits of the species. A list of vice-comital records is given below:

Distribution

var. *media*, including forms with a ratio of length to breadth of subdistal leaves of the short shoots of 1·5–1·8.

V.C. 18, S. Essex: Billericay.

V.C. 20, Herts: Willian (L.), between Buntingford and Royston.

V.C. 23, Oxford: one mile from Banbury on Warwick road, Chalcombe.

V.C. 25, E. Suffolk: S. of Martlesham, W. of Swefling, Woodbridge, Rishangles.

V.C. 27, E. Norfolk: Thorpe-next-Norwich (E.), Postwick (E.), Itteringham (E.), Brundall (E.), Surlingham (E.), Whitlingham (E.), Dunston (E.), Woodbastwick (E)., Walsham (E.).

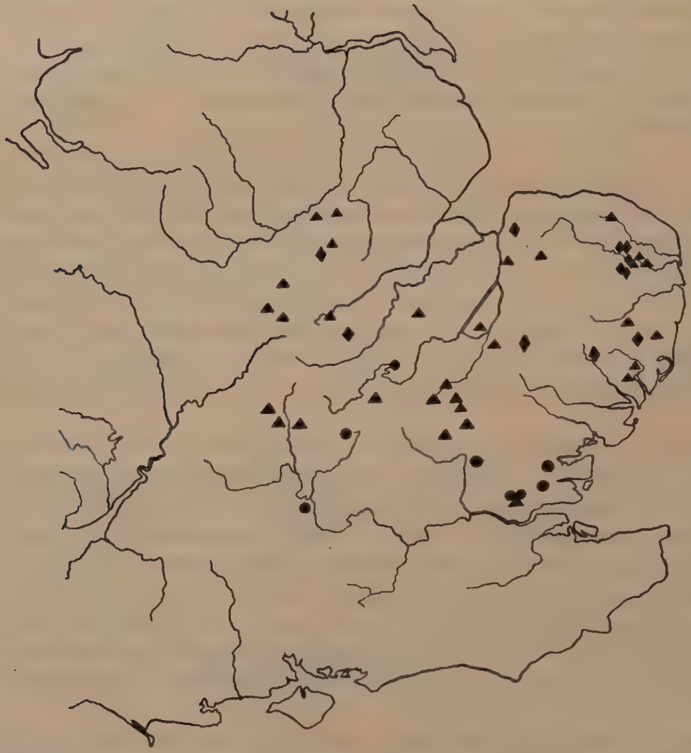

Fig. 5. Map of the distribution of *Ulmus coritana* showing the evidence for the existence of a topocline in leaf shape from north to south. Circles: var. *rotundifolia*; triangles: var. *media*; lozenges: var. *angustifolia*.

V.C. 28, W. Norfolk: Wallington (L.), Swaffham (E.S.E.).

V.C. 29, Cambs: Wicken Fen, ¼ mile W. of Ermine Street on the Tadlow road, and for about three miles along Ermine Street towards Royston, between Witcham and Haddenham.

V.C. 30, Beds: Toplers Hill nr Edworth, Salford (D.).

V.C. 31, Hunts: Sawtry.

V.C. 38, Warwick: nr Burton Dasset.

V.C. 55, Leicester: Langton, two miles N. of Lutterworth (type), 1½ miles W. of Sapcote, ½ mile E. of Cosby, Redmile (F.), Freeby (F.).

V.C. 56, Notts: Owthorpe (F.).

var. *angustifolia*, including forms with a ratio of length to breadth of subdistal leaves of the short shoots of more than 1·8.

V.C. 25, E. Suffolk: Tannington.

V.C. 26, W. Suffolk: Stowupland (type), Tuddenham.

V.C. 27, E. Norfolk: Swainsthorpe, Rackheath, Salhouse (E.), between Mulbarton and E. Cartleton (E.), Norwich (E.), Colney (E.), Caistor St Edmunds (E.).

V.C. 28, W. Norfolk: Appleton (H.).

V.C. 55, Leicester: nr Tilton on road to Market Harborough, between Pickwell and Little Dalby.

var. *rotundifolia*, including forms with a ratio of length to breadth of subdistal leaves of the short shoots of below 1·5.

V.C. 18, S. Essex: ½ mile NE. of Rettendon, Woodham Mortimer, one mile W. of Ramsden Heath, Billericay.

V.C. 20, Herts: Eastwick.

V.C. 22, Berks: E. of Didcot.

V.C. 24, Bucks: two miles SE. of Winslow (type).

V.C. 30, Beds: Westwood, Knotting (M.-R.).

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A Critical Review of the Basic Facts in the History of Cinchona. By Dr Jaime Jaramillo-Arango, former Rector of the National Faculty of Medicine of Bogotá. Forme Colombian Ambassador in London. (Communicated by Dr J. Ramsbottom, O.B.E.

(With Plates **10–21** and 1 Text-figure)

[Read 11 December 1947]

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I. Introduction

The year 1492 stands out as a landmark in the history of the world. In that year, an thanks to the intrepidity of the greatest of navigators, Christopher Columbus, a vast new continent was discovered. This continent was not only destined to become the cradl of twenty-two new nations which in peace as well as in war, as was proved during the last World conflict, have played a vital role in the destiny of the World Community o Nations; but also to bring to humanity the benefit of half a dozen or more new products without which it is doubtful whether the progress achieved during the last five centurie could have been realized.

All of these products have played a definite part in the progress and well-being o mankind, and some have become essential to large groups of the world's population Without *maní*, the subsistence of the African races would be poor indeed. Without the *potato*, which is second in importance only to wheat as a staple diet throughout the world the dietetic needs of Europe could scarcely be met. Not without sentiment and symbolism was a monument erected to that tuber in Braunlage (Germany), with the inscriptio 'The greatest antidote against starvation'. Without *rubber*, we cannot imagine how the development achieved in electricity, transport and communications during the las century could have been accomplished. These three outstanding contributions, not t mention *maize*, an extended and nourishing food, both for human and animal consumption; the *turkey*, which yearly graces our Christmas dinner; the cup of *cocoa*, which some people enjoy as much as the Anglo-Saxons do their cup of tea, and the smoke of the cigarette, cigar or pipe, which we inhale for stimulus or relaxation.

But there is another product which mankind owes to the New World, and the benefit it has derived from this are no less valuable than those which it has derived from the others. This product is *Cinchona*. We will more readily acknowledge its importance whe we realize that malaria is, and has always been one of the most widespread scourges o humanity—800 million people are attacked by malaria every year—and that Cinchona, with the crystalline products extracted from it, was until recent years the only effective remedy against the disease.

The different aspects of the history of Cinchona have for a long time been the subject of innumerable essays. Interest was once again especially focused on them during the second quarter of the present century, when the Tercentenary Celebrations of the first use of Cinchona by the Europeans were held in various countries, particularly in Great Britain and the United States. Moreover, as Weddell has said:

> Peu de sujets en Histoire Naturelle ont eu le privilège d'exciter l'intérêt général à un plus haut degré que le Quinquina; aucun, peut-être, n'a mérité jusqu'ici l'attention de plus d'hommes éminents.

Nevertheless, that history is still in many a particular rather obscure. What is more, on points which are more or less established facts, or which should have been established facts, one often reads statements which not only contradict each other but are themselves contradicted by the actual, unassailable facts, so that one wonders how these could have passed unchallenged for generations.

To endeavour to throw some new light on the early history of Cinchona is the aim of this study. The problems involved are manifold and of absorbing interest.

Did the aboriginal Indians know of the virtues of Cinchona?

How did the Europeans get to know of the properties of Cinchona?

When was Cinchona first introduced into Europe and by whom?

What was the identity of the tree which first bore the name 'Quinaquina' or 'Quinoquino', later given by the Spaniards to the actual genus *Cinchona*?

What is the etymological origin of that word?

Where did Cinchona originate?

Who first wrote about Cinchona in Europe and in England?

How did the first botanical classification of Cinchona come to be made?

II. Did the Aboriginal Indians know of the virtues of Cinchona? How Europeans learned of the properties of Cinchona. The 'Legend' of the Countess of Chinchón. The error of Linnaeus in writing the Countess's name. Why the spelling of Linnaeus must be retained

The first of the above questions, whether the aboriginal Indians knew the virtues of Cinchona or not, is a point that has been the subject of contrary and still unreconciled divergencies of opinion. The answer to it, naturally, depends upon the answer which we give to a closely related question: Was or was not malaria known in America before the discovery of Christopher Columbus?

According to responsible and documented writers, malaria was completely unknown in America before the arrival of the Spaniards, and it was carried to the New World either by the Europeans or by the African Negro slaves. Dr Gualberto Arcos, the famous Ecuadorean historian, on the contrary, asserts that malaria has existed in America from pre-Columbian times, that the disease was rampant in the armies of Pachacutec in the year A.D. 1378, and 'that later it [the bark] was successfully used to treat the intermittent fevers by the tribes of the Paltas and Zaraguros, who administered the bark macerated in *Chicha*' (a kind of fermented maize wine).[1]

Without becoming too deeply involved in this argument, we believe that malaria was a known disease among the American Indians from the earliest times, and that *Cinchona* was familiar to them. The first of these opinions we base upon the fact that, ethnographical remains; anthropological features; linguistic analogies; religious belief, and superstitions, ritual and ceremonial similarities, all support the view that the American races most probably had their origin in the Asiatic peoples. Now, it is known that malaria was present in Asia for many centuries before the Christian era, and we see no reason why these primitive discoverers and colonizers of the New Continent should not have brought malaria with them. Those who take the opposite view, such as Carter,[1] Netolitzky,[2] etc., back their arguments on the facts that pre-Columbian documents (hieroglyphic manuscripts, codices, etc.) do not make any revelation to epidemics which to-day could be assimilated to malaria, and that the early conquistadores, chroniclers, and missionaries of America nowhere suggest, still less mention, that the disease was known there, or that at the time the native populations were experiencing its ravages to a marked degree.

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[1] Arcos, Gualberto, 'Evolución de la Medicina en el Ecuador'. (In *Anales de la Universidad Central de Quito*, 1938, p. 1024).

Without arguing about hieroglyphic documents and writings in unknown languages, whose interpretation is so fortuitous, and observing that, in the same way, those early chroniclers, conquistadores and missionaries do not say anything to the contrary, that the disease was unknown—as neither do they, in general, refer to diseases which certainly must have existed there at the time of the discovery, in the second of the points alluded to, the above-mentioned affirmation is not so absolute: even more, it is rather dogmatic. Moreover, we have it on the authority of Oviedo's *Historia General de las Indias* that the first two settlements that the Spaniards founded on the Mainland, San Sebastián de Urabá and Santa María de la Antigua del Darién, on the Gulfs of the same name, had both to be abandoned one after the other, the first a short time after its establishment, 'under the onslaught of hunger, *fever* and the Indians'; the second, a few years later, because 'on account of its low and marshy site, it was found to be unsanitary': '*Fever became epidemic* and about seven hundred soldiers died within two months'. In other chroniclers' narrations we find that Don Diego de Ordaz, during his exploration of the Orinoco River in 1534, lost more than 300 men '*enfeebled by fever* and other diseases induced by the hot, damp atmosphere of the lower stretches of the river'. Similarly, when Jiménez de Quesada sailed up the Magdalena River in his endeavour to explore the centre of New Granada (Colombia), 'one hundred of them [his men], [a fifth of his force] died during the first weeks', *affected also by fevers*.[3] As a last instance, we have the first-hand evidence of Don Pedro de Alvarado, Governor of Guatemala, who refers to the fact that, when pursuing his design of conquering the northern capital of the Incas, he disembarked in Caráques and marched upon Quito, 'the dense forests and swamps of the Ecuadorean lowlands, the declivities of the Andes, *the fevers of the tropical coast*... presented conditions under which a quarter of the soldiers, a large number of the horses and the greater part of the Indian carriers succumbed and perished'.[3] Malaria 'attacked the troops of Alvarado in the pernicious form termed by Krafft-Ebing, *malarial delirium*, which consists in marked psychic symptoms and terrible excitement'.[4]

As for the original question whether the aborigines knew and used Cinchona, Humboldt, Mutis, Pöppig, Spruce, Markham, etc., and other modern explorers and naturalists who, in the last century, visited the 'Quina Empire', held the view—a remark which was first made by Ulloa[5]—that, because they had found that among the peoples of these regions there not only prevailed a strong prejudice against Cinchona as a cure for fevers, but that many natives would die rather than have recourse to a remedy which they considered so dangerous, the latter were ignorant of the virtues of Cinchona, and that these were discovered by the Europeans. These commentators, nevertheless, seem to have forgotten

[1] Carter, Henry Rose, *Yellow Fever* (Baltimore, 1931), p. 69.

[2] Netolitzky, Fritz, 'Gab es vor Kolumbus die Malaria in Amerika?' *Wien.-Med. Wschr.* Vol. LXXXII (1932), nr. 7.

[3] Moses, Bernard, *The Spanish Dependencies in South America* (London, 1914), pp. 8, 19, 40, 106, 126.

[4] Arcos, Gualberto, op. cit. p. 1053.

[5] Ulloa, Don Jorge Juan y Don Antonio de, *Relacion Historica del Viage hecho de Orden de S. Mag. a la America Meridional &c.* (Madrid, 1748).

two important facts. First, that naturalists like William Arrot, the Scottish surgeon,[1] Jussieu and La Condamine, who visited Ecuador a century earlier, all explicitly state that the current opinion in Loxa was that the qualities and use of the Quina Bark were known to the Indians long before the arrival of any Spaniard. Secondly, that one of the tragic features of the 'Conquest of the New World' was the almost complete extermination in many parts of the native population, so that it cannot be wondered at if, already by the beginning of the nineteenth century, and still more so to-day, the actual country folk nearly everywhere had lost their traditions. Furthermore, it must not be forgotten that Bollus, to whom more extensive reference will be made further on, who lived for many years in Peru, and who wrote the first detailed account of the use of Cinchona in America, definitely affirms that 'the bark was known to the Indians and that they used it upon themselves in disease; but that they always tried with all means in their power to prevent the remedy becoming known to the Spaniards, who of all Europeans particularly aroused their ire.'[2] Bollus goes even further: he states that among the Indians the bark was commonly used for every fever and that the manner in which the Indians employed the bark was in no way different from ours.[3] Finally, it is well to remember also that owing to its bitterness, Cinchona was always one of the most disagreeable of medicines to take, a fact which has created a marked prejudice against it everywhere. Indeed, the former considerations do not mean that the use of the bark was known to all native communities: most probably it was circumscribed to certain tribes, especially in the neighbourhood of Loxa.

As for the highly imaginative stories that the Indians learned of the curative properties of the bark of the Fever Tree by observing that 'fever-ailing mountain lions would chew the bark of a particular tree, which turned out to be the Fever Tree', or that the Europeans learned of it because 'a Spanish soldier who, seized with a fit of malaria in a deserted spot, drank from a lake surrounded by trees bearing the Peruvian Bark, into which some of them had fallen and impregnated the water, thus making a natural infusion, then fell asleep and when he awoke the fever was gone', just because they are so fanciful such colourful legends deserve to survive. It is an established fact, supported by the accounts of the early missionaries and chroniclers, that the Indians were both natural observers and talented botanists, with a wide knowledge of medicinal plants.

With the discovery of the New World, Cinchona, then, came into the *Materia Medica*. And for the first time a given remedy, a *specific*, in the pharmaco-therapeutical sense was introduced into medicine. Strictly speaking, a great and dreaded plague could be combated by individual medicine. The foundation stone of chemotherapy was thus laid. But, what is still more striking, the formula of *quinine* was due to become later the prototype formula on the study of the synthetic chemo-therapeutic drugs that were to come.

The legendary story—with rare exceptions, commonly held in the past as authentic,[4] to-day, thanks in particular to the interesting and documented works of J. Rompel,[5] C. E. Paz-Soldán,[6] and A. W. Haggis,[7] almost proved to be a fiction—as to how the virtues of Cinchona were first known by the Europeans and when it was first introduced to Europe is well worth recording here. Its account not only enfolds a tale of great romantic character but, whatsoever the historical veracity, this version impressed a seal upon a scientific fact, which, in any circumstance, would ensure its transmission to posterity. This fact consists in that—impressed and convinced by the account—Linnaeus wished to immortalize the heroine by giving her name to the genus of the quina tree. With the result that, misinformed as to the correct spelling of the name, he wrote 'Cinchona' instead of 'Chinchona', beginning the word with 'C' instead of 'Ch', as it should have been, an omission to which Don Hipólito Ruiz, in his *Quinologia, ó tratado del Arbol de la Quina, ó Cascarilla* (Madrid, 1792), as well as in the earlier manuscript[1] on which this printed work was based, was the first to call attention, and of which correction Linnaeus himself could never have been aware, for he died the very year (1778) in which Ruiz and Pavón landed in Peru at the head of their celebrated expedition. Since that time, many well-known writers, anxious that the name of the genus should be truly eponymous, as Linnaeus intended, have strongly advocated its correction, but without result.[2] In the last instance, in accordance with the decision of the International Botanical Congress held in London in 1886, to which Markham presented the question, and which voted for retention of the spelling of Linnaeus, and according to the International Rules of Botanical Nomenclature, adopted at the International Botanical Congress of Vienna (1903), thereafter modified by that of Cambridge (1930) and that of Amsterdam (1935), in that which refers to scientific names,[3] the case seems at present definitely settled, in favour of respecting the writing of the learned Swede, the original author of the name. There is no proof—although the presumptive evidence is very strong—that Linnaeus's omission of the 'h' would have been unintentional. Nor is there, even less, any support for the view that it might have been a printer's error, for throughout his numerous works, including the annotated copy in his own writing of his *Materia Medica*, Linnaeus always wrote 'Cinchona'. Only one exception, this time really a typographical error, duly corrected in the 'Errata' at the end of the book, gives support to this last assertion: on page 91 of the 6th edition of the *Genera Plantarum* (1764) the word is written 'Cin*h*ona', that is to say, the second 'c' is missing.

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[1] *Philos. Trans.* (1737–8), p. 81.

[2] Bado, Sebastiano, *Anastasis Corticis Pervviae, Sev China Chinae Defensio* (Genvae, 1663), ch. II, pp. 21–2. Latin text, Appendix, (1).

[3] Bado, Sebastiano, op cit. ch. I, p. 19. Latin text, Appendix (2).

[4] Humboldt alone perhaps, supported by the fact that when he visited Loxa he did not encounter there any reminiscence whatsoever, either verbal or written, on the subject, questioned its authenticity.

[5] Rompel, Josef, *Kritische Studien zur ältesten Geschichte der Chinarinde* (Feldkirch, 1905).

[6] Paz-Soldán, Carlos Enrique, *Las Tercianas del Conde de Chinchón* (Según el Diario de Lima de Juan Antonio Suardo), Lima, 1938.

[7] Haggis, A. W., *Fundamental Errors in the Early History of Cinchona.* Reprinted from the *Bulletin of the History of Medicine*, vol. x, nos. 3 and 4, October and November 1941.

The circumstances which led Linnaeus to commit the error referred to seem to-day to be quite clear. There is every indication that, once he had read La Condamine's *Memoir*,[4] which is known to have been his original source of information, he began to collect as much data as he possibly could about it. As well as requesting some particulars from Bernard de Jussieu, the famous French naturalist and Academician (a letter from Jussieu to Linnaeus dated 26 July 1740, the original of which is in possession of the Linnean Society of London, gives some details about the flowers of the 'Kina' tree, with the reference that 'it belongs to the same order as Coffea, Randia, Nux Vomica, and perhaps Cephalanthus'), he consulted the work of Etienne-François Geoffroy, *Tractatus de Materia Medica*, published in 1741, and that of Sebastiano Bado, *Anastasis Corticis Pervviae, Sev China Chinae Defensio* (1663), which was the first treatise on quina to be published in Europe, and the first to give an account of the 'Chinchón legend'. Both of these important works give the Count's name as 'Cinchon', and there can be no doubt that Linnaeus thought that this was the correct spelling of the name.[5]

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[1] *Compendio Historico-medico Comercial de las Quinas.* (Botanical Department, British Museum (Natural History).)

[2] Among these, Sir Clements R. Markham's plea *A Memoir of the Lady Ana de Osorio* (1874), is one of the most brilliant.

[3] Sect. 13. Orthography of names. Art. 70: 'The original spelling of a name or epithet must be retained, except in the case of a typographical error, or of a clearly unintentional orthographic error.'

[4] Condamine, Charles Marie de la, 'Sur l'Arbre du Quinquina', *Histoire de l'Académie Royale des Sciences* (Année 1738), pp. 226–43.

[5] Haggis affirms (p. 448) that 'it was from Bado's work that Linnaeus, when naming the genus, adopted the spelling "Cinchona", as is proved by the bibliographical notes in Linnaeus's own writing contained in the annotated copy of his *Materia Medica* of 1749' (vol. I, p. 24); in the possession of the Linnean Society of London. However, with the kind co-operation of Mr S. Savage, Librarian of the Society, we have examined minutely the source referred to without finding any proof for such an assertion. Moreover, as the writing of Linnaeus is so small, we have had taken an enlarged photograph

Bado, himself an Italian physician, claims to have taken the story from a letter, written in Italian in 1649, by Antonius Bollus, a Genoese merchant, who for many years lived in Peru. This being the case, Bado wrote the name of the Count 'Cinchon' instead of 'Chinchón', either, most probably, because in the original letter of Bollus the name was spelt in that manner (unfortunately it has not been possible to trace the original of that letter, neither does any copy exist), or (and the same reflexion applies also to Bollus) by reason of a phonetic imposition of the language: in Italian the sound 'Ch' before 'i' is given by 'C' and not by 'Ch' as in other languages. 'Ch' before 'i' in Italian is pronounced 'K'. With the logical deduction that one of the two (Bollus or Bado) who heard the name 'Chinchón', whether aware or not of its exact Spanish spelling, had to write it 'Cinchon' to ensure a correct pronunciation by his Italian readers.

The original story, collated with the most authoritative sources, runs as follows. About the year 1630, Don Juan López de Cañizares, Corregidor of Loja, Audiencia of Quito, in the Jurisdiction of the Ancient Vicekingdom of Peru (to-day a province of the Republic of Ecuador), fell ill with an intermittent fever. A friend of the Corregidor's, a Jesuit missionary named Juan López, advised him to take the native remedy which had cured him of a similar fever some thirty years before. This had occurred in the village of Malacatos, some leagues south of Loja, where an Indian Cacique, baptized into the Catholic faith as Pedro Leiva,[1] had administered the remedy to him and told him that the Indians had employed it for many centuries against fever. The Corregidor agreed to try it, and an infusion of the bark of the 'Fever Tree' was given to him, whereupon he made a rapid recovery. Some time later (1632?–1638?), in Lima, Doña Francisca Henríquez de Ribera, wife of his patron, the Viceroy Don Luis Gerónimo Fernández de Cabrera Bobadilla y Mendoza, Fourth Count of Chinchón, was attacked with the same fever. On hearing this news, the Corregidor wrote to the Viceroy sending him a portion of the bark, informing him of its wonderful properties, giving him directions for its use and 'expressing his almost certain hopes that it would cure the tertians of his Wife'. When the Viceroy showed his wife this letter she immediately agreed to try the remedy. Whether Dr Juan de Vega, the Viceroy's personal physician, was consulted, the original narratives do not state, but it is natural to suppose that he was. This point is of interest because some writers, Joseph de Jussieu among them, from whom the version of the cure of the missionary and the Corregidor originates, maintain that it was Dr de Vega who, either because he knew of the Corregidor's case, or because the bark had been sent to him personally, suggested its use to the Viceroy; others, on the contrary, affirm that the Viceroy asked the Corregidor to Lima in order to instruct the Vicereine's physicians in the correct method of preparing and administering the medicine, and that this was first tried on patients of inferior rank.

The Countess was completely cured:

> When this was learnt in the City, the people approached the Vicereine by intermediaries, not so much joyfully and in congratulation, but in supplication, begging her to deign to help them, and say, if she would, by what remedy she had at last so marvellously, so quickly, recovered, so that they, who often suffered from precisely this fever could also provide for themselves.
>
> The Countess at once agreed. She not only told them what the remedy was, but ordered a large quantity of it to be sent to her, to relieve the sufferings of the citizens, who often suffered from the fever. Nor did she only order this great remedy the Bark to be brought, but she wished to dispense it to the many sick with her own hands. And the thing turned out

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of the page in question—which we reproduce in this work (Plate **10**). Even this reveals no positive support for Haggis's suggestion. As for the annotations which appear on both sides of the page (dates, historical references, pharmacological data, etc.), a careful study of these shows that they were taken by Linnaeus from Geoffroy's work (Art. VI, *De Cortice Peruviano Kinâ Kinâ dicto, et Cascarillâ*, pp. 179ff.) and not from Bado, although it is obvious that Geoffroy himself was indebted to Bado for many details.

[1] Arcos, Gualberto, op. cit.

so well that, just as she herself had experienced the generous hand of God in that miraculous remedy, so all the needy who took it marvellously recovered their health. And this bark was afterwards called *Countess's Powders*, which in Spanish is *los polvos de la Condesa.*[1]

The above legend, as we have said before, has now been almost completely discredited particularly by the works of Paz-Soldán and Haggis. To refute it, modern writers[2] base their argument on two fundamental points: (*a*) the fact that in no contemporary writing on the Quina Tree (Fever Tree) or on contemporary events in America, is there a single reference to this legend; (*b*) that in the Official Diary of the Count of Chinchón, kept by his clerical secretary Dr Don Juan Antonio Suardo, preserved in the General Archives of the Indies in Seville,[3] there appears no mention of that circumstance. This Diary records in minute detail every activity and interest of the Count, and has frequent allusions to the Countess, but nowhere is there any reference of her ever having been attacked by intermittent fevers. On the contrary, throughout the period covered by this Diary (15 May 1629 to 30 May 1639), the Count seems to have been the one who suffered periodically from 'chills and fevers', from 29 April 1631, when '...for His Excellency being worse with a tertian fever, the physicians had him bled in the evening', first definite allusion to his repeated attacks of malaria, up to the end of 1638, when on 21 October he again developed fever '...whereof he was bled twice'. To assign the cure of the Countess to the year 1638 as Markham does—and other writers do after him—is to act against all historical evidence, and entirely arbitrary.

In his Introduction to Suardo's Diary[4] Father Rubén Vargas-Ugarte suggests that this omission is due to the fact that the illness and cure of the Countess took place before the Diary was started, that is, in effect, during her journey from Paita to Lima. Let us examine this possibility. The Count and Countess touched at Paita on October 1628. Owing to his wife's pregnancy, the Count decided she should continue the journey to Lima by land while he went on by sea to Callao. The Countess did not arrive in Lima until 19 April 1629. During her overland journey, her son was born in Lambayeque on 4 January 1629. The Count disembarked at the port of Callao on 18 December 1628, and entered Lima on 14 January 1629. The Diary was begun on 15 May 1629, i.e., less than a month after the Countess's arrival in Lima. The illness and complete cure of the Countess should then have taken place during the lapse comprised between October 1628 and 15 May 1629. And the 'aboriginal remedy' then, was not administered at the suggestion of the Corregidor of Loja or the Jesuit Father Diego de Torres Vásquez, as it has hitherto been asserted, but on the advice of some person or physician whose name is unknown—a proposition which is within the range of probability, but which still remains to be proved. As far as we know, there is not any documentary evidence for such a thesis. But, admitting its possibility, then why, we ask, if the drug brought such 'marvellous' results in her case, was it never administered to the Count who, during ten years of office so frequently appeared 'ill and weary', owing to the 'chills and fevers...which were diagnosed by the physicians as tertians'?

A legend so charming as the one of the Countess, however, is abandoned only with reluctance and some writers have tried to alter the story in a very plausible way, to fit the new evidence against it. The distinguished Peruvian medical historian Dr Paz-Soldán,[1] for example, suggests that the person cured with the bark sent from distant lands was the Count and not the Countess, and that if he ventured to take the unknown remedy, which represented a real therapeutic adventure, it was not on the advice of his physicians, but yielding to the affectionate entreaties of his devoted wife and nurse who, full of anxiety and despairing of the orthodox remedies, induced him to take the bark sent from Loja. This version weaves the sentimental legend of the Countess in a different pattern. Unfortunately, the arguments put forward by the writer of this engaging story are merely conjectural, such as the fact that according to 'reputable historians', the Count, 'having received marked favour from our Lady of the Prado, decided to build a church in her honour and gave for this purpose 80,000 pesos', and that later he sent the Virgin other presents from Cartagena evaluated at 100,000 pesos. The most signal 'favour' would precisely have been to free him from malaria through the 'aboriginal remedy'. As to the gifts of the Count, they are easily explained, for we know, on the one hand, how fervent and devout a Catholic he was, and on the other, something of his state of mind when he landed for the second time in Cartagena, for within a few hours he had to withstand the shock of his wife's sudden death. Indeed, it is not unlikely that the presents sent from this town may have consisted of the jewels and personal apparel of the Countess.

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[1] Quotation taken from A. W. Haggis's translation of a passage of S. Bado, *Anastasis Corticis Peruviae, &c.* (1663).

[2] Outstanding among these writers were the Jesuit Father Bernabé Cobo, one time Superior of the College of Pisco and Rector of the Community's House in Arequipa, and the Augustine Father Fray Antonio de la Calancha. Between 1596, when he left Sevilla, and 1657, when he died in Lima, Father Cobo spent sixty-one years in the New World, chiefly in Venezuela, Colombia, Peru and Mexico. His great work, published for the first time in 1890–3, *Historia del Nuevo Mundo*, is the best work on this subject at the time. In 1633, Father Calancha published his *Coronica Moralizada de la Orden de San Avgvstin en el Perv*, in ch. IX of which, while referring to the 'excellencies and abundances' of that land, he notes that the use of the bark of the Fever Tree 'has produced miraculous results in Lima'.

[3] Legajo 50–de la Audiencia de Lima. Archivo General de Indias (Sevilla).

[4] Vargas-Ugarte, S. J., Rubén, *Diario de Lima de Juan Antonio Suardo* (Lima, 1935).

Furthermore, as we have seen from the Diary, the Count suffered from 'chills and fevers' practically throughout his period of office (1629–39), for which again and again he was bled, a treatment neither physically nor psychologically the easiest to endure. Not once is the bark, or the 'Fever Tree' mentioned in any part of this Diary, notwithstanding the fact that, had the Viceroy taken it, with or without the advice of his physicians, they could not have failed to remark upon the result, not only because of the rank of their patient, for whose health prayers were sometimes offered up in the Churches of Lima, but because of the evil and extension of the disease and the lack of any effective remedy for it.

The above being the case, if we consider the version of Dr Paz-Soldán, then the cure of the Count must have taken place after the date last given in the Diary, 30 May 1639, and before the Viceroy's departure from Lima, in June 1640,[2] a period of which no record remains. This seems very improbable and there is no evidence to support it. Indeed, one of the most surprising features of the whole problem is that, although as early as 1633, Father Calancha, as we have shown, was writing that the bark 'has produced miraculous results in Lima', no attempt was made in the following six years to administer it to the Count himself, who was 'languishing' from malaria. Perhaps this omission can only be explained when we remember the prejudices that dominated medicine at that time.

Other well-known versions of the circumstances in which quina took hold of the imagination of the Europeans or of the 'Legend' of the Countess of Chinchón, are worthy of a critical mention.

Le Poëme du Quinquina,[3] an ode to the drug in two cantos of 28 pages each, written by La Fontaine at the request of *Uranie*,[4] name meant to identify the Duchess of Bouillon, and dedicated to her, is a composition which, if in more than one respect is worthy of admiration, in truth adds but little to the reputation of the famed fabulist, neither does it shed any new light upon the history of the medicament. One amongst all of La Fontaine's remarks in this poem is of interest to mention: it is that the discovery of quina was far more valuable than the treasures that the Spaniards were so anxiously searching for in the New World, treasures upon which, we could add, by one of fate's ironies, the conquistadores were never able to lay their hands.[1]

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[1] Paz-Soldán, Dr Carlos Enrique, *La Introducción de la Quina en Terapéutica* (México, 1941).

[2] *Consultas del Consejo y Cámara* de Indias. Legajo 762 de Indiferente General (Sevilla). Letter of Don Jerónimo Gómez de Sandoval, dated in Cartagena, 1 December 1640.

[3] Poëme / du / Quinquina, / et autres Ouvrages / en Vers / de M. de la Fontaine. A Paris. Chez Denis Thierry (1682).

[4] One of the nine Muses, daughters of Jupiter who presided over the Arts: *Clio* for History; *Eutherpe* for Music; *Thalia* for Comedy; *Melpomene* for Tragedy; *Terpsichore* for Dance; *Erato* for Elegy; *Polymnia* for Lyrical Poetry; *Urania* for Astronomy; *Calliope* for Eloquence and Heroic Poetry.

Rendons graçe au hazard; cent machines sur l'onde
Promenoient l'avarice en tous les coins du monde:
L'or entouré d'écueils avoit des poursuivans:
Nos mains l'alloient chercher au sein de sa patrie,
Le Quina vint s'offrir à nous en même tems,
Plus digne mille fois de nôtre idolatrie.
Cependant, près d'un siècle on la vû sans honneurs.

There is *Zuma ou la Découverte du Quinquina*,[2] the melodramatic tale of Madame de Genlis, governess of the children of Philippe Egalité, Duke of Orleans, translated into various languages and which has also been performed as a play. If this tale has many admirable qualities from a literary point of view, it has no historical basis whatever and must be regarded as the product of a lively imagination.

The narration of Don Ricardo Palma, *Los Polvos de la Condesa*,[3] rests essentially on versions based upon the relations of Bado, Jussieu, La Condamine, and other early writers. The appreciation of its historical value is enfolded in the critical judgement we have made of the 'Legend of the Countess'.

La Santa Virreina,[4] a drama in verse by José María Pemán, first produced in 1939, and which has also been played in various parts of the world, is a piece fundamentally based upon a Spanish translation of *Zuma*, made in 1931 by Dr Francisco J. Blanco-Juste.[5] According to Markham,[6] there exists another Spanish translation of *Zuma*, of 1827, under the title *Zuma, ó el Descubrimiento de la Quina, novelda Peruana*. If, just as with *Zuma*, *La Santa Virreina* is a work of undeniable literary value, and apart from that it is a beautiful elegy to the missionary and colonizing work of the Spaniards, it derives, naturally, like the first, from a fiction and does not contribute any element of value to the problem of the history of the origin of the Europeans's knowledge of the virtues of quina.

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[1] The three great treasures of America, which the Spaniards most feverishly coveted, that of *Cuzco*, that of *El Dorado* and that of *Moctezuma*, it is known, escaped their ardent chase: the secret of where the treasure of Cuzco was hidden was for ever lost when, at the death of Huascar and Atahualpa, sons of the last Imperial Inca Huayna Ccapac—the first murdered by order of his brother, the second murdered by order of Pizarro—their descendant, Carlos Inca left Peru in exile; that of El Dorado was never found; and that of Moctezuma fell into the hands of the pirate Giovanni da Verazzano, alias Juan Florentin.

[2] Genlis, Mme la Comtesse de, *Zuma ou la Découverte du Quinquina*. Dédié a Mme la Comtesse de Choiseul (née Princesse de Bauffremont) (Paris, 1817). Briefly recapitulated, Madame de Genlis's story runs as follows. The Countess of Chinchón is stricken with an intermittent fever; she is dangerously ill. Zuma, the most beautiful of all Indian maidens around Lima, whom the Countess had taken into her service, in possession of the secret which all the natives and she in particular, had sworn never to reveal to the Spaniards (the last resort in the hands of the natives to avenge themselves on the hated invaders was to watch them die helplessly of malaria), distressed upon seeing her mistress, for whom she had developed a great affection, at death's door, owing to the disease for which such an infallible remedy existed, determined to give the Countess, furtively, during the night, some of the precious powder which her husband, with the consent of the Indians, had smuggled into the Palace to Zuma, to cure her of the same fever. Zuma is caught in her action. In the belief that the disease afflicting the Countess was due to a slow poisoning (tacitly, Madame de Genlis held the physicians of the time in little esteem), caused by the potions secretly given her by her maid with the intention of killing her, Zuma and her husband are condemned to be burnt at the stake. Roused by the unusual commotion in the Palace, having somewhat improved and with a presentiment of the impending tragedy, the Countess makes an effort to reach the scene of the execution in time to save the young Indian couple at the very moment when the stake was to be set alight. As an act of gratitude for the action of the Countess in favour of Zuma and her husband, the Caciques come forward to reveal the virtues of the bark.

[3] Palma, Ricardo *Tradiciones Peruanas. Los Polvos de la Condesa.* Crónica de la época del décimocuarto Virrey del Perú.

[4] Pemán, José María, *La Santa Virreina.* Poema dramático (Madrid, 1939).

[5] Blanco-Juste, Francisco J., *Zuma en el descubrimiento de la Quina.* La Voz de la Farmacia (Madrid, 1932).

[6] Markham, Sir Clements, R., *A Memoir of the Lady Ana de Osorio* (London, 1874), p. 43.

The recent historical study by Mrs M. L. Duran-Reynals,[1] a work which we have reviewed recently,[2] is an attractive and animated work which shows clearly that the author has read widely in the relevant literature. Some of the chapters are of absorbing interest. Unfortunately, it cannot be considered an exhaustive historical study of the subject, for apart from its imaginative fiction, it is not, as the dust-wrapper claims, 'true in every detail': it contains no few inaccurate statements and wrong dates.

III. When was Cinchona first introduced into Europe and by whom?

In connexion with the first part of the question, as we have already pointed out and to which more detailed reference will be made in the following chapter, we have the clear evidence of Father Antonio de la Calancha that by 1633 the powdered bark of the Fever Tree had already 'produced miraculous results in Lima'. Knowing the zeal of the Spaniards in acquainting the mother-country with the novelties of all kinds which they were finding in the New World, of which there are hundreds of examples, it is logical to assume that, at least from that date onwards, they did not fail to send to Spain or to Rome, reports on and samples of this bark. Such an assumption is strengthened by the fact that it concerned an antidote for a disease which was widespread and endemic in Europe, and a disease against which the medicine of the time was helpless, reasons for which it constituted for both the medical and official world a cause of constant preoccupation. As '*opprobia medicorum*' was the disease then known. To set the date at which Cinchona (the genuine antimalarial bark, *Cinchona vera*), was introduced into Europe between 1630 and 1635 is therefore very approximate. However that may be, further mention will also be made of the fact that there exists authoritative evidence, such as that of Dr Villerobel, that by 1639 Cinchona was already in use in Spain (Dr Barreda's case), and that even then it was already being sold in some ports.

As for who first introduced Cinchona into Europe, as a result of recent investigations the possible answers to this question have had to be drastically revised.

Some writers, who accepted the Chinchón legend, have contended that it was the Countess herself who, in gratitude for her cure, wishing that its benefits should be enjoyed in the mother-country, took a quantity of the bark with her when she returned to Spain. These authors, however, ignored the fact that the Countess never reached Spain for—according to a letter dated in La Havana, 28 February 1641, of Don Jerónimo Gómez de Sandoval,[3] Commander of the Fleet in which the Viceroy was making his return journey from America—she died and was buried in Cartagena, Colombia, on 14 January 1641, the day after the Fleet had put in at that port from Puertobelo (Panamá). An epidemic, it seems, had broken out on board, as Gómez de Sandoval reports at the same time that the greater part of his crew was ill. The Countess, most probably, was herself a victim of this epidemic.

The greatest confusion on this point has resulted from the erroneous accounts of Sir Clements R. Markham, who incidentally, consistently confused the Count's first wife, Doña Ana de Osorio,[4] who died before he went to Peru, with his second wife, Doña

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[1] Duran-Reynals, M. L., *The Fever Bark Tree.* First published in U.S.A. in 1946 and republished in Britain in 1947.

[2] Jaramillo-Arango, Jaime, 'The Fever Bark Tree: The Pageant of Quinine'. *The Medical Bookman and Historian* (London, February 1948).

[3] *Consultas del Consejo y Cámara de Indias.* Legajo 762 de Indiferente General. Archivo General de Indias (Sevilla).

[4] Markham, Sir Clements R., op. cit.

Francisca Henríquez de Ribera, who accompanied him to Lima,[1] and asserted that on her return to Spain the Countess distributed samples of the bark to the students of the University of Alcalá de Henares (p. 62), where, in 1639, it was first used in the treatment of Dr Miguel de Barreda, Professor of Theology. On referring to this last assertion, which Markham suggests having taken from a letter of the noted Spanish physician, Dr José Villarobel (*sic*), to Bado, we find that Dr Villerobel makes no mention of the bark being distributed to the students of the University, but merely states that in 1639 Dr de Barreda was treated there with bark which had been given to the University.

According to other writers, Dr Juan de Vega was the person responsible for bringing the bark to Europe, and some go so far as to assert that this distinguished practitioner made a fortune with it by selling it at Seville at 100 reales the pound. Here again, as Haggis has shown, all the documentary evidence is against such a story. Dr de Vega, the first man to lecture on Medicine in the New World (1635), never returned to Spain but settled in Lima, where he held the Chair of Medicine in the University of that city. For ten years after the Count of Chinchón's departure for Europe—he embarked at the Port of Callao on 2 June 1640—de Vega's signature continues to appear on official documents of that University.[2] The shaky lines of the signature of the later dates betray his advanced age.

Yet another suggestion which has been advanced is that it was the Count of Chinchón himself who first brought it back with him to Europe. This does not bear investigation for a moment, for the Count did not return to Spain until 1641—the Armada bringing him, sailed into the Bay of Cádiz on 1 July of that year,[3] and already by that date, as Dr Villerobel's statement to Bado testifies, the bark was not only fairly well known in Spain, but was even commonly sold in some places.

In his not very accurate account of the discovery of Cinchona,[4] Aristides A. Moll alludes to 'a quotation by Father R. Vargas-Ugarte, editor of Suardo's Diary, of a letter by the General of the Jesuits, Rev. Mucio Vitellecchi [*sic*] in 1630, in which he refers to the Countess's recovery through the Jesuits' help, and also mentions the receipt of a supply of "the drug" [used in her case]'. Moll does not give his authority for this statement. The quotation is to be found in an article which the author contributed to the *Revista Histórica* of Peru, entitled "*1631–1931. Una fecha olvidada. El tercer centenario del descubrimiento de la Quina*".[5] Father Vargas-Ugarte also fails to state his sources. We have found, however, what appears to be the pertinent part of the letter in question, quoted in Alessandro Canezza's *Gli Arcispedali di Roma* (1933). Translated into English, the relevant passage reads as follows:

> Great satisfaction was caused by the news of the cure of Her Excellency the Countess of Chinchón obtained through the help of our colleagues. Thus has Our Lord caused to be rewarded the generosity of their Excellencies towards our Company and particularly towards their confessor, to whose suggestion is due the good [result] obtained. We have received

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[1] Don Felix Cipriano C. Zegarra first pointed out, in the *Revista Peruana* of 1879, that it was the second, and not the first wife, who accompanied the Viceroy to Lima. Definite confirmation of this fact is given by Dr Francisco Javier Blanco-Juste, in his *Historia del Descubrimiento de la Quina* (Madrid, 1934), where he published a photographic facsimile of the official death certificate of Doña Ana de Osorio, who died on 8 December 1625, three years before the Count's appointment as Viceroy.

[2] These documents are preserved in the Archivo General de Indias, Sevilla.

[3] *Consultas del Consejo y Cámara*..., op. cit. Letter dated 1 July 1641, of the 'Presidente y Jueces Oficiales de la Casa de Contratación de Sevilla' to the 'Consejo de Indias'. Archivo General de Indias, (Sevilla).

[4] Moll, Aristides A., *Aesculapius in Latin America*. (31, 'An Epoch-making Discovery', p. 188.) (Philadelphia, 1944).

[5] Vargas-Ugarte, S. J., Rubén, *Revista Histórica*. Tom. IX. Entregas II y III, 1935. pp. 291–301.

from the F. Procurator a certain quantity of the medicine which we shall not fail to test.[1]

Canezza states that the letter is addressed to Father Nicola Mastrilli, Provincial of Peru, but, here again, the complete text, date and present whereabouts of the original letter are not given. No definite conclusion, therefore, can be based on this document as long as the relevant facts concerning it are unknown. So far, notwithstanding exhaustive research, we have been unable to find the original or a complete copy of it. According to Father José Teschitel, S. J., Keeper of the Archives of the General House of the Jesuits in Rome, no trace of this letter is to be found there. We have written to the Archives of the Provincials of Peru, trying to find if the original is there or if there exists any reference to it. We have not had a reply yet.

However, it is of interest to note that in the same work, the author tells us that the first sample of the bark only arrived in Rome in 1632, when it was brought by Father Alonso Messias Venegas, who was sent to Rome with the office of Procurator, to report on the Missions of Peru to the General of the Order. Should the letter bear the date 1630, the contradiction between what is stated in it by Father Muzio Vitelleschi and what he (Canezza) affirms, could not have escaped the notice of that distinguished historian. Father Nicola Mastrilli, to whom Father Vitelleschi is supposed to have addressed the letter, is, in fact, Father Nicolás Durán Mastrilli who, from 29 December 1629[2] to 1635 and then again from 1639 to 1645[3], was Provincial of Peru. Father Vitelleschi, as is known, died in the latter year.

Meanwhile, our refutation of the legend of the Countess's cure still stands.

Sir Humphrey Rolleston,[4] Dr J. Ramsbottom,[5] and other writers state that it was Father Bernabé Cobo, to whom we have and will refer more extensively further on, who first, in 1632, introduced Cinchona into Europe. The same claim had previously been made by Rompel in the article that he contributed to the *Catholic Encyclopaedia* (New York, 1910, vol. VIII, p. 373), 'Jesuits' Bark'. Neither Father Cobo's biographers, nor any 'History' of the Jesuits in America, make any such claim, and there is no record of Father Cobo having returned to Europe during the sixty-one years he spent in the New World. Furthermore, it is known[6] that in 1632 he was in Mexico, where he stayed for more than nine years.

Finally, a more recent statement on this problem calls for our attention.

Not long ago, in an essay on quina,[7] Dr Virgilio Paredes-Borja, a distinguished Ecuadorean physician, Professor of Anatomy of the Central University of Quito, wrote as follows:

> The activity of the Jesuits has no rest, the Jesuit Father Alfonso Mesías Venegas introduced quina into Italy in 1642, Cardinal de Lugo became interested in the new drug and at the Congress of the Order in 1649, the powder of the quina bark is distributed through the good offices of the Brothers who returned to their Provinces, and thenceforward people began to talk of the 'Powders of the Cardinal', this being the name by which the powder of the quina

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[1] Canezza, Alessandro, *Gli Arcispedali di Roma*. (Capitolo XIX, *Spezieria*, Le Premizie della Corteccia di china, pp. 89–90) Roma, 28 Ottobre 1933. Original text: 'Grande soddisfazione ha recato la notizia della guarigione ottenuta dalla Ecc. ma Contessa de Chinchón per mezzo dei nostri confratelli. Cosi ha destinato N.S. a premiare la generositá degli Ecc. mi coniugi verso la nostra Compagnia e specialmente verso il loro confesore, al cui suggerimento risale il bene conseguito. Abbiamo ricevuto dal P. Procuratore una certa quantitá del medicamento che non si mancherá di sperimentare.'

[2] Vargas-Ugarte, S. J., Rubén, op. cit. p. 37.

[3] Astrain, S. J., *Historia de la Compañia de Jesús en la Asistencia de España*. Tomo V (1615–52). Madrid, 1916, pp. xi and 418.

[4] Rolleston, Sir H., 'The History of Cinchona and its Therapeutics'. *Ann. Med. Hist.* (1931), vol. III.

[5] Ramsbottom, J., 'Jesuits' Bark'. *Nat. Hist. Mag.* (January 1931), vol. III, no. 17.

[6] González de la Rosa, M., *Colección de Historiadores del Perú*; I. P. Cobo, *Historia de la Fundación de Lima* (Lima, Mayo de 1882).

[7] Paredes-Borja, Dr Virgilio, *Contribución del Ecuador a la Materia Química: la Quina*. Revista de la Casa de la Cultura Ecuatoriana. 3, Año II (Enero-Diciembre 1946), p. 217.

bark was designated. Appointed Pope, with the name of Innocent X, Cardinal de Lugo ordered Gabriel Fonseca, in 1668, to examine the curative effects of quina and after the issue of his report, it was provided in the Pharmacy of the Medical College.

Aiming to discover the authority on which it is stated that it was the Jesuit Father Alfonso Mesías Venegas (*sic*) who, 'in 1642, introduced quina into Italy', and that 'appointed Pope with the name of Innocent X, Cardinal de Lugo, directed Gabriel Fonseca, in 1668, to test the curative effects of quina and following his report gave it to the Pharmacy of the Medical College in Rome', we have asked Dr Paredes-Borja by letter for information on the matter. He kindly referred us to Celli's work on Malaria, and to the contributions of Prof. Enrique F. Scrimaglio in the *Revista de Historia de la Medicina de El Rosario* (Chile, 1942).

With reference to the first part of the above assertion, that referring to Father Alonso (or Alfonso) Mexia y Venegas, or Messia Venegas, Celli[1] only states that he took that information from the studies of Alessandro Canezza, but does not mention Canezza's sources. In fact, it is true that Canezza, in the work already quoted,[2] says that Father Messia Venegas was the one who, in 1632, brought the bark with him to Rome, but, he does not produce any documental proof in that respect. There is, nevertheless, in that particular, a very suggestive fact: that is, that Suardo in his Diary, on 29 July 1630, writes: 'This day, the Congregation of the Fathers of the Company of Jesus appointed as their General Procurator of the Province, Father Alonsso Messia, to go to Rome in the following year, to report on the state of the Missions to the General of the Order'; then, on 31 May 1631: 'This day, at 5.30 in the afternoon, the Royal flagship set sail for Tierra firme,...and on this occasion, Father Alonsso Messia, Procurator General of the Province, left for Rome....'[3] On the other hand, it is known that Father Messia's journey to Rome took nearly a year.

We have not been able to find Prof. Scrimaglio's work.

As for the second part of the statement, for which Celli is not entirely responsible, he does not invest Cardinal de Lugo with Papal rank, we find it impossible to make it accord with the following indisputable facts:

(*a*) That Cardinal de Lugo never occupied the Chair of St Peter. Pope Innocent X was Juan Bautista Pamphili, and the three Popes who reigned between 1643 when Father de Lugo was elected Cardinal, and 1660, the year of his death, were: Urban VIII, who conferred upon him that honour (1623–44); Innocent X (1644–55) and Alexander VII (1655–67).

(*b*) That Cardinal de Lugo, as above-mentioned, died in 1660. Both Markham's and Celli's statements that parcels of Cinchona were first sent to Cardinal de Lugo, and distributed by him, around the year 1670, are therefore incorrect as well.

In the last instance, the most plausible theory regarding the question seems to be that, if perhaps independently, at one time or another, a chance traveller or navigator may have brought samples or even a cargo of the real fever bark with him to Spain or Italy as a speculation, the Jesuits were the ones who first deliberately sent or brought it to Rome, where they enthusiastically acquainted their countryman, the already famous Father de Lugo (from 1643, the Illustrious Spanish Cardinal Juan de Lugo), with its 'surprising virtues'. And it was this Prince of the Church, Protector of the Church and City Council of Lima, who (himself, after having been 'lying at the point of death', was cured with it[4]—among other acts, by requesting the Pope's physician, Gabriel Fonseca, another Spaniard, to test the new remedy; following the latter's highly favourable report, distributing the bark free to the poor in his house or Palace and also in the Pharmacy of the Collegio Romano (not the *Medical College* of Rome) in charge of the lay brother of the Community, Pietro Paolo Puccerini, and in the Hospital of the *Santo-Spirito* in Rome and, in 1649, at the death of the General Father of the Society, by recommending it to the IXth Provincials' General Council of the Order, gathered in Rome to elect a new General Father, as a powerful asset against malarial fevers, and one which would be of inestimable aid to the Fathers in their missionary work throughout the world) initially contributed most powerfully to its recognition and distribution in Europe. The synonyms 'Jesuit's Bark'; '*Pulvis Patrum Scil. Jesuitarum*'; '*Pulvis Jesuiticus*'; '*Pulvis Eminentissimo Cardinal de Lugo*'; '*Pulvis Lugonis*'; '*Pulvis Cardinalis*' or 'Cardinal's Bark', by which the remedy was first most commonly known in Europe enhance this suggestion.

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[1] Celli, Angelo, *The History of Malaria in the Roman Campagna* (1833), pp. 157–8.

[2] Canezza, Alessandro, op. cit. p. 90.

[3] Vargas-Ugarte, S. J., Rubén, op. cit. pp. 73, 133.

[4] Bado, Sebastiano, op. cit. Account of Bollus's letter, p. 24.

Almost conclusive confirmation of the above view appears to us to be provided by the famous Aretine philosopher, physician, naturalist and poet, Francesco Redi (1626–98). In his work *Esperienze Intorno a Diverse Cose Naturale, e Particolarmente a quelle, che ci vengon portate dall' Indie*, a work which was published in the form of a letter addressed to the famous Jesuit Father Athanasius Chircher (Kircher),[1] and printed for the first time in 1671 in Florence, Redi writes:

> There are still new experiments to be made on the *Calumba* root, credited to be a great alexipharmac; on the Vanilla, and on the woods of Laor, and Solor, which also being very bitter, it would be reasonable to believe they really have all those singular characteristics which Writers attribute to them, but that in fact do not appear evident, as I always see very evident the effects of the marvellous bark of that Peruvian tree from the mountains of Guajachil, bark commonly called *China China*, and by the Spaniards *Cascarilla de la oja*, used to check and combat the attacks of quartan, simple tertian, double and continuous fevers. For this the whole World owes a debt of gratitude to those Fathers of your most venerable Order, who were the very first, much to their glory, to bring it to Europe.[2]

Another fact established beyond all doubt, is that quina started to arrive regularly in Italy from Peru in 1647. And that it was Father Bartolomé Tafur, appointed Procurator of the Province on 2 April 1642, who first brought a fairly large consignment of the bark with him, when at the death of Father Vitelleschi, Superior of the Community, he visited Rome in 1645 in order to attend the VIIIth General Congregation of the Order, due to elect a new Superior. For the first part of this statement, we have the authority of Pietro Paolo Puccerini, to whom we have already referred, and who, at the time was for more than fifteen years Apothecary of the Pharmacy of the also above-mentioned Collegio Romano, Institution located in the Via del Caravita, between the Church of San Ignazio and the door of the actual Conservatory. In a statement signed and dated 5 April 1659, written for Bado, and published by him in his work, Puccerini writes:

> ...I the undersigned have full and sure faith...and can moreover state that this Bark, which has been sent to me from Peru from the year 1647 up to the present, has—so to speak—accomplished miracles....For the sake of the truth I must place this on record. Further, His Eminence the Very Reverend Cardinal de Lugo, of our Company, has a large Case of Vows, which testify that this Bark can be given to all, as it has been noted that all who used it have been cured. In faith thereof I have of my own hand drawn and signed this statement, upon which I appose the seal of our Pharmacy.[3]

For the second part, there exists the affirmation of Father Honoré Fabri (Antimus Conygius),[4] and Badus,[5] and it is recorded in the Acts of the Congregation, that Father Tafur was present at its opening in August 1645.

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[1] Father Kircher, Professor of Physiology at the University of Würzburg, was the first, with Antony van Leeuwenhoeck, to apply the microscope to the study of the smallest beings, 'invisible to the naked eye', in which they suspected the cause of diseases, and to describe bacteria and protozoa.

[2] *Opere di Francesco Redi.* In Venezia, Scritta dall' Abate Salvino Salvini, 1771. Vol. II, pp. 69–70. Italian text, Appendix (3).

[3] Bado, S., op. cit. Cap. XXIII, p. 240. Italian text, Appendix (4).

[4] Conygio, Antimo, *Pvlvis Pervvianvs Vindicatvs de Ventilatore, &c.* (Romae, 1655).

[5] Bado, S., op. cit.

IV. Confusion regarding the Tree to which the name 'Quinaquina' or 'Quinoquino' was first applied

Whatever the final accurate solution to the problem as to who first introduced Cinchona into Europe and at what date—somewhere in the *Archivo de Indias* of Seville, in the Archives of Peru and New Granada (Colombia), the Vatican Library or the General Library of the Society of Jesus in Rome, there must be a relevant document, so far undiscovered, which could lead to the final clarification of this problem—no doubt most of the confusion in regard to this subject arose from the fact that the majority of the early naturalists and commentators, who dealt with the matter in Europe, confused and mistook the actual *Cinchona* genus for the *Myroxylon peruiferum* or *Peruvian Balsam Tree*. This last is the tree from which is extracted the resin of the same name and whose bark was considered at the time to possess febrifugal properties against tertian and intermittent fevers (agues), products and virtues which were known in Europe prior to the introduction of 'Cinchona Bark'.

The aggregate facts that a regular trade in the bark of the Balsam Tree, or *Quinaquina* as it was then called, was carried out between Europe and America before the advent of *Cinchona* (Peruvian Balsam already appears on a list of merchandise of the city of Worms, in Germany, in 1609), and that, added to the medical analogies referred to, there unquestionably exist some botanical similarities between the two trees, were the main factors responsible for the general confusion which prevailed at the time on the whole question. For, when the growing rumour of the astonishing febrifugal properties of the 'Peruvian Bark' began to spread in the Old World, the medical fraternity, on the one hand, misled by the little they knew about it, regarded the 'new Peruvian remedy' as the bark already familiar to them. While the merchants, on the other hand, eager to enhance the prestige of their old stock, which was already then declining in popularity, continued to refer to the new and genuine antimalarial bark with the same name as the primitive one, that is to say, by the name of *Quinaquina*. The bad conditions in which, owing to the rudimentary methods of packing and to the delay in transport, the bark at first commonly reached Europe, as well as the action of the native collectors of the product who, with the unexpectedly great demand for the 'Fever Bark', took advantage of the similarities mentioned, by surreptitiously and indiscriminately mixing the two barks, according to their convenience, as is natural, did not promote the elucidation of the problem.

That the Peruvian Balsam Tree (*Myroxylon peruiferum*) and the Fever Tree (*Arbol, Palo o Leño de Calenturas*; *arbor febrifuga peruviana*; *lignum febrium*; *lignum vitae*) are two distinct trees and that the name 'Quina-Quina' was given by the natives to the first of these, is a fact which can be deduced unmistakably from the description of the first historians and naturalists who went to America.

Three early accounts provide us with unique and incontrovertible evidence on this point.

(1) Father Antonio Vázquez de Espinosa, a barefooted Carmelite missionary, was born in Jerez de la Frontera in the last third of the sixteenth century and died in Seville in 1630. Prior to 1622, he lived at least twelve years in America, travelling from Mexico as far south as Chile. In his contemporaneous manuscript *Compendio y Descripcion de las Indias Occidentales*, a kind of detailed chronological report of the countries and regions he visited, a document now in possession of the Vatican Library (Barberini Collection, No. 3584), he writes:

Second Part. Book V.

Cap. 26. In which continues the description of the district of this city [Chuquisaca or Villa de la Plata: to-day Sucre, former capital of Bolivia], and in particular of the quality of the trees and their timbers.

> 'Of all the trees referred to in the preceding chapter, only the palm bears coconuts, the walnut very tough-shelled nuts, the carob carob-beans like those of Spain, although they differ in being white and sweeter...the quinaquina tree likewise bears other pods like the carobs; the other trees do not bear fruit.
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> . . . .
>
> 'From the quinaquina tree is extracted a liver-coloured resin very fragrant and healthful, with its vapours chills and head colds are consumed, with this resin mixed with oil wounds and sores are cured, and the oil which is extracted from its seeds has the same effect and is more efficacious. The quinaquina tree is very beautiful and its wood is very fragrant and strong, the colour of its wood is white and tawny veined.'[1] [Plate **11**.]

In ch. 21 of the same manuscript, in which he describes the city of La Plata, its foundation, locality, environs, population, etc., Fray Antonio says that it is established in the Province of Charcas, so called from the name of the Indians who inhabited it; and that the Indians living there speak the Quichua language, which is the lingua franca of the Incas.

These remarks, in our view, demonstrate that the Province of Charcas (Plates **12** and **13**) —a fact which is confirmed by a similar observation to that of Fray Antonio Vázquez de Espinosa made by Father Bernabé Cobo—must have been, so to say, one of the natural habitats of the Quina-Quina tree (Balsam Tree).[2] They show also that the name 'Quinaquina', which Fray Antonio uses only in his work in the chapters quoted (25 and 26), must have a Quichua origin, for this was the native language of Charcas. We intend this last remark for those who doubt that this word derives from that language.

(2) For his part, Father Bernabé Cobo, in his masterly work already referred to,[3] gives the following description of the Quina-quina tree, which on the whole agrees with that of Fray Vázquez de Espinosa, and, like this one, unmistakably reveals that by that name the natives referred to the Balsam Tree, that is, the *M. peruiferum* of to-day's Linnæan classification:

> Quina-quina they call in Peru a large and beautiful tree, resembling a medium-sized olive; the leaf of the size and shape of that of a Ceuta lemon-tree; the trunk is reddish, resinous and aromatic. The tree is calid in the second degree, styptic and dry and of a soft smell. Grows as seeds some almond-sized pips, yellow in colour and of an oleaginous nature, that with fragrance smell pleasantly; they too are calid and styptic in the second degree, and dryer than the first. Scarifying the trunk and branches drops a fragrant resin, that coagulates so much, that it can be ground to a dark grey powder, which is calid and dryer than the seeds. This tree grows in the hot lands of the Province of Charcas. If the teeth are often cleaned with the bark, it tightens and soothes them; and the shavings from the wood boiled with Polypodium, Senna and anis leaves, and the decoction taken some mornings before breakfast, clears the stomach, liver and spleen, clears and cleanses the bladder. The pounded leaves applied upon fresh wounds, dries and closes them, and the decoction of them with brine, leaves of *Chilca* and *Molle* reduces the swelling of the gouty legs. From the seeds of this tree a marvellous oil, for fresh wounds is made, which is much used in Potosí.[4]

It is worth pointing out here how both Fray Antonio Vázquez de Espinosa and Father Cobo speak of the 'marvellous oil' which is extracted from the seeds of that tree and which is very widely used for external application to wounds by the inhabitants of La Plata and Potosí, both towns within the district which later became the Audiencia of Charcas.

Father Cobo's description, on his part, corresponds almost literally to that given by Don Pedro de Osma,[5] in a letter dated from Lima, 26 December 1568, and addressed to

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[1] Spanish text, Appendix (5).

[2] Haggis's sketch in his work (op. cit. p. 428), locating Chacas or Charcas in Ecuador is erroneous on that point.

[3] Cobo, Bernabé, op. cit.

[4] Cobo, Bernabé, op. cit. Lib. VI, Cap. LXXXI, p. 88. Spanish text, Appendix (6).

[5] Don Pedro de Osma y de Xara y Zejo.

Dr Nicolás Monardes in Seville, one of the most outstanding medical figures of the Spanish Golden Age. Dr Monardes in his turn speaks of the juice or principle of this tree, which is obtained by incision or decoction and which, according to this learned man, taken three or four times half an hour before the chill 'taketh a waie the colde, in three or foure tymes that they doe it'. The illustration of the fruit of this tree included in Dr Monardes's book *Historia Medicinal de las Cosas que se traen de nuestras Indias Occidentales que sirven en Medicina*, a work whose first part was published in 1564, and the full text in 1574, does not leave any doubt whatever that this is one of the many species of *M. peruiferum* known at present.

Don Pedro de Osma writes:

> Most Worshipful Sir, and Most Renowned Doctor.
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> . . . .
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> ...Also I doe sende your worship a fruite, whiche is of greate profite, and these Trees bee not founde in any countrie but in this countrie, thei are of the greatnesse of an Oke, of those in Spain, it hath many vertues for the rinde, beyng made in pouder, and caste into any soare, which is needful to bee made cleane, it maketh cleane: and afterwards maketh the fleshe to growe, and healeth it. And rubbyng the teeth with this pouder, it maketh them cleane very well, and put upon the gummes, the fleshe beyng taken awaie, it doeth fleeshe them, and the teeth whiche be lose, it maketh them faste. Seethyng the leaves of this Tree well in water, and washyng with the water any maner of swellyng, whiche hath any sore, or that it be cankered, it taketh awaie the swellyng, and impostume. And puttyng some small linen clothes, weate in seethyng warme upon the medicine, whiche is put upon the fore, or upon the pouder that is made of the rinde: it maketh the soares to heale more quickly, makyng that there come no humour to them. Of the saied Tree commeth out a Rosine, whiche is of sweete smell, that doeth serve to perfume in many deseases, of the hedde, and to make plaisters for many evilles, and I do sende it to your worshippe. Of the fruite the Indians dooeth make certaine drinke, which is for them verie healthfull, your worshippe maie commande to sowe theim, for I would bee glad that thei should growe, for it will bee a thyng of much delight, for the profite that it dooeth in Phisicke, and for the noveltie of the Tree, for in all tymes it hath a very good smell....[1]

If even more conclusive evidence were needed for the assertion that by the name 'Quinaquina', the aboriginal Indians referred to the Peruvian Balsam Tree, we have the description of Don Hipólito Ruiz, the learned Spanish Botanist who, at the Head of the Botanical Expedition, in 1777, was sent out by Charles III to study the Natural History of the Kingdoms of Peru and Chile. In the final and unpublished copy of his *Relacion historica del Viage,...á los Reynos del Perú y Chile &c....*, work which we are in the process of transcribing for publication, Don Hipólito writes:

> Myroxylon peruiferum v. [vulgo] *Quinoquino*: a very high and leafy tree, with a thick trunk, smooth and straight, ash-coloured, as are all its branches. The bark is of a white straw-like colour on the inside and according to the greater or lesser amount of resin with which it is impregnated it is more or less granulated, compact and heavy, and of a colour sometimes reddish, at other times yellowish, or again dark chestnut; finally in its smell and taste it is balsamo-aromatic, similar to the golden Peruvian Balsam which under the name of white Balsam is sold in the Pharmacies and Drugstores. The resin which is collected from the Quinoquinos is called in Peru *Estoraque*: they fumigate rooms with it, and also use its Fruits, called Pips or Seeds of Quinoquinos, which together with the bark reduced into powder are mixed with animal fats or resins, and applied in plasters to relieve headaches. The fresh leaves pounded heal recent wounds, and the Balsam and bark are considered as being admirable balsamics and vulneraries. From the fruit is made the Oil called *Quinaquina*: taking ounces of the fruit well pounded, these are infused in a 'quartillo' of wine [equivalent

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[1] Quotation from John Frampton's translation of Dr Monardes's book and published in 1577 with the English title *Joyfull News out of the New Founde World, Medicinal Historie whiche doethe treate of the Thinges that are brought from our Occidental Indias, whiche doethe serve for the use of Medicine.* Spanish text, Appendix (7).

> to 504 c.c.] for twenty-four hours, thereafter it is boiled over a gentle fire with a pound and a half of common Oil until it is dry, then is added one pound of turpentine and lastly one ounce and a half of incense and as much again of myrrh. They say that this Balsam has wonderful results for wounds of the breast, that it dries ulcers and wounds. Of the trunk the Indians cut poles, and they prefer these to those of other trees for their strength and long endurance. At the extremities of the branches of the Quinoquinos, as being farthest from the trunk, and preferring these to those of other trees, the Birds *Poccochycuys*, *Kcuychis* or *Hediondos* build their nests, to preserve their little ones or eggs from the Monkeys and other animals who climb the trees in search of food.[1]

(3) On the other hand, independently, both Father Cobo and Father Antonio de la Calancha give in their works a description of the Fever Tree, the *Cinchona* genus of to-day, which singularly agree with each other. Cobo writes:

> Of the fever tree
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> In the neighbourhood of the City of Loja, diocese of Quito, grows a certain kind of large trees, which have bark like the cinnamon, a little more thick, and very bitter; which, ground to powder, is given to those who have fevers and with only this remedy they leave them. These powders must be taken in quantity to the weight of two 'reales' in wine or any other liquid somewhat before the appearance of the chill. These powders are now so well known and esteemed, not only in all the Indies, but in Europe, that they are pressingly requested from Rome.[2]

Father Antonio de la Calancha writes:

> There grows a tree which they call the fever tree in the country of Loja, whose bark, of the colour of cinnamon, made into powder amounting to the weight of two 'reales' and given as a beverage, cures fevers and tertians; it has produced miraculous effects in Lima. There grows cassia-fistula in abundance, sarsaparilla...the *quinaquina* a general remedy (either in seeds, or melted into a mass) for various kinds of pains of the head and body, and of all wounds; the quina seed is like those of the mustard, though it is white and not round, an efficacious medicine against fatigue of the body, and dangers of spasms; the pincopinco, universal remedy for various diseases....[3]

A comparison of the preceding texts reveals how Father Cobo and Father Calancha agree in a surprising manner in that the 'Fever Tree' is native to the Province of Loja; in that it has bark of the colour of cinnamon; in that this bark ground up in doses of the weight of *two reales* (old silver coin) is used against fevers and tertians, and finally, in that the fame of the remedy is extraordinary in the Indies. Furthermore, upon attentively reading the text of Father Calancha, it can be seen that he, like Father Cobo and Fray Antonio Vázquez de Espinosa, refers to 'Quinaquina' as a separate tree from the 'Fever Tree'.

With all this indisputable contemporary evidence it can no longer be assumed that the natives in America shared the confusion about the two different barks we have under review, which existed among European physicians in the seventeenth and early eighteenth centuries, particularly the first. It seems positive also, that the European merchants themselves, who had direct or indirect contact with the native sources, knew more clearly what they were about, for when the Loxa bark began to be imported to the Old World they gave it the name *Cascarilla*, which means 'small or thin bark' and implies an established difference from some 'large or thicker bark' with which they were already familiar. The men employed in collecting the bark were known as *cascarilleros*.

[1] Ruiz, Don Hipólito, *Relacion historica del Viage, que hizo á los Reynos del Perú y Chile el Botánico dr. Hipolito Ruiz en el año de 1777 hasta el de 1788, en cuya epoca regresó á Madrid*. MS. in the Library of the Botanical Department, British Museum (Natural History). I have printed for the first time, in the *Bulletin of Spanish Studies*, University of Liverpool, January and April issues (1948), the valuable chapter on Lima. The chapter on the Province and City of Huánuco de los Cabelleros will appear in the next issue of the *Revista Javerina* of Bogotá (Colombia). Folio 65 (4). Spanish text, Appendix (8).

[2] Cobo, Bernabé, op. cit. Lib. VI, Cap. XCVII, p. 100. Spanish text, Appendix (9).

[3] Calancha, Fray Antonio de la, op. cit. Lib. I, Cap. IX, p. 59. Spanish text, Appendix (10).

In this connexion it is worth pointing out here that the quotation from Francesco Redi, to which we have already alluded, contains a curious reference. He states that the Spaniards called the fever bark from Guayaquil *Cascarilla de la oja*. This points to a confusion which would have been natural to Redi and other writers who used that name, particularly Italians. The correct Spanish name was, of course, *Cascarilla de Loja*, which Redi and others heard and wrote as *Cascarilla dell' oja*.

An interesting observation also first made by Don Hipólito Ruiz, both in the MS. of the final copy of his *Relacion historica del Viage,...&c.* and that of his *Compendio Historico-medico Comercial de las Quinas,* was that the natives of Peru commonly used to designate the Balsam Tree by the name of *Quino-quinos*, and the bark and fruit by that of *Quina-quina.* At the present time, in the country these names have been transferred from the Balsam to the Cinchona Tree, the vernacular for which is *Quino* or *Quino-quino*, and the bark *Quina* or *Quina-quina. Quinquino* and *Quinquina* are both contractions of the original word. The forest of *Quinos* is designated as *Quinal* or *Quinar.*

V. Etymological origin of the word ‘Quina’ or ‘Quinaquina’

The etymological origin of the word ‘Quina’ or ‘Quinaquina’—both words are used indiscriminately in medical literature—has been the subject of different interpretations. In his Memoir *Sur l'Arbre du Quinquina*, already mentioned, which he sent from Ecuador to the Royal Academy of Sciences of Paris, where it was read in July 1738, La Condamine[1] suggests its derivation from the word *Quina-ai*. This word he states to have found in an old dictionary of the Quichua tongue[2] printed in Lima in 1614, and he gives the Spanish meaning as ‘Mantelilla India’, a kind of cape or shawl with which the Indians covered themselves. The Quichua vocabulary, in the opinion of the same author, being a very limited one, he concluded that this word may have come to be used, by analogy, for the bark which is the cloak or covering of the tree. The bark, within this line of thought—although this is not an observation of La Condamine—would have constituted for the Indians the bark *par excellence*, or ‘Bark of Barks’ (cortex corticorum). Like most suggestions of amateur etymologists, La Condamine's explanation is too plausible and picturesque to be true.

Haggis, in the classic paper to which we have referred so often, tells us that he not only has consulted the dictionary referred to by La Condamine but also an earlier edition of 1604, both of which are in the British Museum. In neither edition could he find the word *Quina* or *Quinaquina*, but neither could he find La Condamine's word *Quina-ai*. The only words at all similar to be found in either dictionary, he states, were *Quinray-lliella* in that of 1604 and *Quinaay-lliella* in that of 1614. Both editions give the same meaning for these words, that is, ‘Mantellina de india’, which in English means ‘an Indian head-shawl’.[3]

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[1] Charles Marie de la Condamine, the learned French astronomer and mathematician, was a member of the Scientific Expedition that, composed of Pierre Bouguer, Louis Godin and himself, with the main purpose of determining the curve and shape of the earth in relation to the Poles, by measuring the arc of a degree of the meridian in the neighbourhood of the equator, went to Ecuador and spent three years in Quito (1736–9). From there, La Condamine later went to Lima, and travelled extensively through Peru. Although not a professional botanist, La Condamine availed himself of the opportunity of his stay in Ecuador, to study all the facts relative to the celebrated quina bark and embodied the results in the Memoir referred to. As will be seen, the official botanist to this expedition, Joseph de Jussieu, also wrote a very fine study of the Quina tree which remained unpublished until 1936.

[2] The General Language of Peru, or of the Inca, as it was first named by Fray Domingo de Santo Thomás.

[3] Haggis thinks (p. 422, footnote no. 18) that the ‘r’ in ‘Quinray’ is a printer's error for ‘a’: that is, that the word should really be ‘Quinaay’ as it appears in the 1614 edition. We have found the word printed as ‘Quinray’ in the 1586 and 1603 editions of what we believe to be the same dictionary, as well as in other dictionaries, not only in conjunction with ‘lliclla’ but in cognate compounds. We therefore believe ‘*Quinray*’ to be the correct spelling and that the single example of ‘Quinaay’ in the 1614 edition results from a printer's error in which ‘a’ has been printed for ‘r’. (See Plate **14.**)

Moreover, adds Haggis, the word 'lliella'[1] appears independently in both vocabularies, and its meaning is given as 'Manta de India, la que cubre la saya', or, in English, 'an Indian mantle which covers the skirt'. This meaning being almost identical with that of the compound word suggested to Haggis that the suffix alone bears the full significance implied by the double word. From his own source—we continue quoting Haggis—it is thereby shown that La Condamine's deduction is erroneous.

On his part, based upon the fact that in both editions of the vocabulary he consulted[2] the name '*Quinua-Quinua*' is to be found, with the Spanish equivalent given as 'a certain leguminous plant thus called'; in that the fruit of the Balsam Tree has at first sight the appearance of a legume (=fruit or seeds that grow in pods), and in the long known fact that in Quichua the duplicate word very commonly suggests a substance, tree or plant thought to possess remedial virtues or any other striking particularity, such as being poisonous, but primarily the first condition, Haggis attributes the origin of the word '*Quina-Quina*' to the Quichua word '*Quinua-Quinua*'.

We support Haggis's view of La Condamine's theory, for surely to derive the word 'Quina', in French 'Quinquina', from the compound word 'Quinaay-lliclla', the only one that appears in the 1614 Dictionary referred to (Plate **14**)—and no other Quichua vocabulary of the same date is known—as having the meaning to which La Condamine alludes ('Mantelilla India' for 'Mantellina de india': in Spanish the two expressions have a certain homology), involves a process of bisection hardly justified in etymological science. Nor do we wish to dispute Haggis's affirmation upon the medical significance that the duplicate names very often had for the Indians, of which we could give numerous instances.[3]

However, we have some critical remarks to offer to Haggis's identification of 'a certain leguminous plant thus called' with the Balsam Tree. The Indians most certainly must have been familiar with many leguminous plants, and it is doubtful whether the Balsam Tree was the only tree whose fruits had the appearance of a legume. Why, in applying a name to a tree so well known to them and so greatly valued by them for its properties, should they have chosen to refer to it by a 'metaphor' or 'homology', by such a nondescript and unsatisfactory term of distinction based upon the character of its fructification? *Quinua, quinua* or *Quinuaiquinua* (that, as is shown by the photographs which accompany this study (Plates **15** and **16**) is actually how respectively the word appears in the 1604 and 1614 editions of the Vocabulary in question[4]) = 'a certain leguminous plant thus called'; from which, the tree whose fruit resembled a legume, is the original 'Quinaquina' or *Myroxylon peruiferum* of the aboriginal Indians: the argument is not very convincing. Concerning this word, furthermore, if in the above-mentioned Vocabulary, and even in an earlier one, of 1586, the word appears duplicated, with the meaning of 'a certain leguminous plant thus called', in the 1603 edition, the entry is made in the simple form, i.e., as 'Quinua', with exactly the same meaning.

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[1] When writing of the single word, or of the compound with that suffix, Haggis refers to the word as 'lliella'. In all the dictionaries we have consulted, including those used by Haggis, the word appears written as 'Lliclla', with 'c' instead of 'e'. And 'lliclla' is the real Quichua word. Of the corresponding Spanish pronounciation 'lliclia', Don Hipólito Ruiz writes: 'it is a piece of woollen, cotton or other material of the size of a square *vara* [80 sq.cm.] adorned with various stripes of different colours, and some embroidery with bands of gold and silver and a fringe of the same material. They [the Indians] carry them upon the shoulders, fastening them over the breast with a *Timpis*, which is a bodkin or similar object which assures it holding together, as if it were fastened with a large pin.' Don Hipólito Ruiz, op. cit. Footnote. Folio 24 (4): Spanish text, Appendix (11).

[2] Owing to the circumstance of not making any mention as to authorship and that it was printed by the well-known printer of the time, Francisco del Canto, the 1614 edition has been erroneously attributed to the latter. The author of both editions seems most probably to be the Padre Maestro Fray Juan Martínez, of the Order of St Augustine.

[3] As, for example, *chaucha-chaucha*, herb against swellings of the spleen, liver and womb; *chullco-chullco*—its roots masticated, applied in a poultice, are used for dissolving goitres; *cilla-cilla*, herb against bronchitis and asthma; *huarmi-huarmi*, plant which is an emmenagogue; *macha-macha*, plant whose fruits intoxicate; *moco-moco*, emetic and stimulant of uterine contractions; *moho-moho*, carminative plant, anti-epileptic and digestive; *pila-pila*, herb to comb one's hair with to make the hair grow; *pinco-pinco*, herb for various disorders: used locally, it joins, dries and heals wounds, it welds the fractures of bones; masticated, it cleanses the teeth marvellously and also combats diarrhoea; *pulla-pulla*, remedy to mature abscesses and to resolve tumours; *puntu-puntu*, remedy against side-aches; *puru-puru*, remedy against stains and blotches of the face and wound scars; etc., etc.

[4] The second 'i', in the word *Quinuaiquinua*, might be a misprint, and might correspond to the comma (,) which divides the compound word *Quinua, quinua*: at least it also appears written in this last manner in the 1586 edition, to which we will make detailed reference further on in our work.

To come back to La Condamine: he must have felt wherein lay the weak point of his argument, for he excuses it by asserting that the Quichua vocabulary was very limited. In judging the Indians incapable of assigning an individual and distinctive term to the Balsam Tree, Haggis, by implication, follows him in this. As a matter of interest, we have personally computed the number of words in Fray Juan Martínez's Quichua Vocabulary: it contains 5008 words. And that of Father Diego Gonzalez Holguín, of the Company of Jesus, edited also in the 'City of the Kings' (Lima), in 1608, by Francisco del Canto, contains more than 12,000. The average vocabulary of a well-educated Englishmàn contains some 5000 words; of a writer or professor some 10,000 words; basic English is founded on 850: and English has one of the richest vocabularies in the world. From this comparison it will be manifestly seen that the inferences of La Condamine and of Haggis, implicating paucity of vocabulary, have no real weight.

Is there any other etymological alternative for the words 'quina' or 'quinaquina', with which at present the bark of the 'Fever Tree' (*Arbor febrifuga peruviana; lignum febrium; lignum vitae*) is specifically designated, and with which the natives, it is to-day beyond doubt, referred to the Balsam Tree? In our efforts to discover the etymological origin of this word 'Quinaquina' we have examined all the early Quichua vocabularies and dictionaries which are extant,[1] but we must confess that the results have not been commensurate with our efforts. As far as it has been possible for us to carry out our research into the matter, there remains only one other alternative which might deserve consideration and be worthy of further investigation, although this alternative is also susceptible of a weighty objection. In all four editions of the Vocabulary which we attribute to Fray Juan Martínez, we found two words which have hitherto hardly been mentioned. They are: '*Queñua*', given in all editions as a '*Tree thus called*', and '*Queñuaqueñua*' designation for a '*Grove of this* [tree]' (Plate **16**). Father de Torres Rubio's Vocabulary also gives this word '*Queñua*', with the same meaning '*Tree thus called*'. If, in transcribing these two words into Castilian, it is borne in mind (*a*) that, according to the established habit, the letter 'e' of the first syllable of various Quichua words beginning with '*Que*' has generally been substituted in the spoken and written language by an 'i'—thus the original name of the language of the natives is not 'Quichua' but 'Quechua': from '*Quecchua* or

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[1] (*a*) S. Thomás, Domingo de, *Lexicon, o Vocabulario de la lengua general del Perú.* Valladolid, Francisco Fernandez de Cordoua (1560).

(*b*) (Martínez, Fray Juan, (?), Gonzalez Holguín, Padre Diego, (?)), *Arte y Vocabulario en la lengua general del Perú llamada Quichua, y en la lengua Española.* 'En los Reyes' (i.e. Lima), Antonio Ricardo (1586). (This vocabulary was the one ordered by the Provincial Council which, by a Decree of the Council of Trent, met in Lima in 1583.)

(*c*) (Martínez, Fray Juan, (?), Torres Rubio, Padre Diego de, (?)), *Grammatica y Vocabolario en la Lengva General del Perú, llamada Quichua, y en la lengue Española.* Seuilla: Clemente Hidalgo (1603).

(*d*) Martínez, Fray Juan, *Vocabulario en la Lengua General del Perú llamada Quichua, y en la Española, neuvamente emendado y añadido de algunas cosas que faltavan.* 'En los Reyes', Antonio Ricardo (1604).

(*e*) Gonçalez Holguín, Diego, *Vocabvlario de la Lengua General de todo el Perv llamada lengua Qquichua, o del Inca.* 'En la Ciudad de los Reyes', Francisco del Canto (1608).

(*f*) (Martínez, Fray Juan, (?)), *Arte, y Vocabulario en la Lengua General del Perú llamada Quichua, y en la lengua Española.* 'En los Reyes', Francisco del Canto (1614).

(*g*) Torres Rubio, Diego de, *Arte de la lengua Quichua. Breve Vocabvlario qve Comiença por los uocablos Quichua al trocado del pasado.* Lima, Francisco Lasso (1619).

Also later dictionaries such as those of Father Honorio Mossi de Cambiano (1860), of Don Luis Cordero (1895) and others.

Most of the dictionaries listed above are now extremely rare. Copies of them are to be found: of

Qquechua'=name of a nation, which extended over five provinces; hot land; quechua tongue; inhabitant of a hot land (various commentators); from '*Quechhua*', temperate land (Fray Juan Martínez); from '*Qquechhua*', 'temperate land or of hot temperament' (Padre Gonzalez Holguín); and, (*b*) that, according to medieval custom, in the old Spanish way of writing, as in all languages, the sign or tilde placed over a vowel or over the letter 'n', had the value or conveyed the sound of an absent 'n' or 'm', similarly, the Spanish 'ñ' would be equivalent to a double 'n' (nn), phonetically in modern Castilian '*Queñua*' should be written '*Quinnua*' and '*Queñuaqueñua*', '*Quinnuaquinnua*'.

On the one hand, however, the dictionary of Father Gonzalez Holguín has the word '*Qquiñua*', which is probably equivalent to our word 'Queñua', and defines it as a 'tree of puna good for fire-wood and coal'. Obviously, this cannot refer to the Balsam Tree, for the word '*puna*', also of Quichua origin, means 'very cold climate or temperament', while the Balsam Tree is a tree of 'temperate land or hot temperament'.

On the other hand, this '*Qquiñua*' of Father Gonzalez Holguín's dictionary seems to be identical with the tree, of an entirely different species from the Balsam Tree and the Fever Tree, described by Father Cobo and Don Hipólito Ruiz.

Father Cobo's account is as follows:

> Of the Quínua
>
> The Quínua is a tree of the size of an Olive and from there downwards until it grows no more than the height of a man; it has red branches and trunk, with the bark very thin, that peels easily...it is a tree so strong in resisting the rigours of cold and frosts like the Quishuar; and so, only these two species of trees grow in the rigorous páramos [highlands] of Peru, especially in the Provinces of Collao. They make of the Quínua very good coal, which is very necessary where it is so cold.[1]

And Don Hipólito Ruiz writes:

> Passing through various Mineral Works and Lagoons, we descended to the Ravine of the *Quinua*, (a name acquired) because many trees grow in it called *Quinuares* or *Quinhuares*: which serve as a great auxiliary to the Miners of the Cerro de Yauricocha for the buildings and Mine works due to the strength of their trunks, and (for being) the wood of great duration for the fire. From this tree we established the genus *Polylepsis*, a name derived from the numerous thin layers in the (ma)nner of papers the colour of molasses, in which its bark peels progressively in proportion to the years it has.[2]

(*a*) in the British Museum, the Bibliothèque Nationale (Paris), and in the Library of Prof. Paul Rivet; of (*b*) in the Bibliothèque Nationale; of (*c*) in the Bodleian Library (Oxford); of (*d*) in the British Museum, the Bibliothèque Nationale, and in the Library of Prof. Paul Rivet; of (*e*) in the British Museum, and in the Library of Prof. Paul Rivet; of (*f*) in the British Museum, and the Library of Prof. Paul Rivet; of (*g*) in the British Museum, the Bodleian Library, and in the Library of Prof. Paul Rivet.

Furthermore, naturally, copies of various of these vocabularies exist in the National Libraries of Madrid, Washington and Berlin; in the Vatican Library; in various National Libraries of the Latin American Republics, in those of various Religious Communities and in private collections.

Although the 1586, 1603 and 1614 vocabularies do not reveal the name of the author, not only by the similar, almost identical titles, but also by the similitude of the texts, we believe that the author of these three is also Fray Juan Martínez, author of that of 1604. In the relatively short time which elapsed between the publication of these vocabularies, Fray Juan Martínez would not have dared to publish with his signature a work which was not his own, nor would any contemporary publish spuriously and anonymously a work of which the legitimate author was still living.

Sir Clements R. Markham, for his part (*The Incas of Peru*, 1910, pp. 312–13), suggests that the vocabularies of 1586 and 1603 are by the Jesuit Fathers Padre Diego Gonzalez Holguín and Padre Diego de Torres Rubio respectively: however, he does not give any proof for his assertion.

[1] Cobo, Bernabé, op. cit. Libro VI, Cap. CXXIII, p. 124. Spanish text, Appendix (12).

[2] Ruiz, Don Hipólito, op. cit. Folio 35 (4). The syllables or words in parentheses are missing from the finished copy, but are in the draft-copy of the same MS., also in possession of the Library of the Botanical Department of the British Museum (Natural History), from which it can be clearly deduced that while transcribing his work, by involuntary oversight, Don Hipólito omitted to write them. Spanish text, Appendix (13).

Then, to summarize the facts implicated in this hypothesis, if the words *Queñua* and *Queñuaqueñua* were to be synonymous with 'Quina' and 'Quinaquina', among the aborigines two separate trees must have borne the same name, and ought to have been distinguished by some other specification: one of 'cold temperament', good for fuel, and another of 'temperate climate', used for its medicinal properties.

We add some final words on other Quichua designations which are said to have been applied to the Cinchona bark.

The Quichua word for 'chill and fever', according to Father Domingo de Santo Thomás,[1] is *chucchu*, and the 'bark of the tree', in the same language, is *cara*. By adding these two simple words the Indians would have formed the compound one *cara-chucchu* and thus called 'the bark of the tree against chills and fevers'. This was first noticed by Joseph de Jussieu, official botanist to the expedition of Godin, Bouguer and La Condamine and brother of the two other great botanists Antoine and Bernard, in his *Memoir* on the quina,[2] the first really technical study on the subject. Although according to the editor, Jussieu's study was written in 1737,[3] it was not published until 1936, two centuries later. Doubtless the misfortune of Jussieu's loss of reason while still in America accounts for the long obscurity in which his valuable work lay forgotten.

Jussieu writes:

> They call it *yara chucchu cara chucchu*. *Yara* means tree, *cara* the bark, *chucchu* cold of the fever so to say the tree of intermittent fever. They also call it *ayac-cara*, which means bitter bark.[4]

The Quichua words for 'bitter thing', 'bitter', 'bitterlike', we have found in early Quichua vocabularies, are actually *hayac* for the first one (Fray Juan Martínez), *hayasca* or *hayásccapa* for the two last (Fray Domingo de Santo Thomás).

Chifflet,[5] Colmenero,[6] Heinrich von Bergen,[7] and other writers, affirm that the natives called the Quina Tree by the names '*Gannanaperide*', '*Gannaperide*' or '*Guananepide*'. If that is so, they surely cannot mean by 'natives' the 'aboriginal' Indians, as the letter 'G' did not exist in the Quichua language, a sufficient reason for these names not appearing in any of the classical Quichua vocabularies.

VI. Who first wrote about Cinchona in Europe and in England?

It has been generally accepted, and almost universally repeated, that the first European work to deal with Cinchona was the *Vera Praxis* of the Spanish doctor Pedro Barba, Professor in the Royal Academy of Valladolid. Our investigations of this claim reveal that it must have been made without reference to the work in question, for even the wording of the title varies with the different authorities. In Waring's *Biblioteca Therapeutica* (1878) it is quoted as *Vera Praxis ad curationem Tertianae &c.* Dr Blanco-Juste, Professor of Pharmacy in Madrid University, gives it as *Tratado de la fiebre por la Quina.* The *Illustrated Spanish Encyclopaedia* (1930) enters the title as *Tratado de la curación de las fiebres por medio de la quina.* Other writers refer to Barba's work as *Vera Praxis* or *Vera Praxis ad curationem.* Whatever they consider to be the correct title, they all refer to the same work, for as far as is known Barba was the author of only one publication on the subject: this is the *Vera Praxis / de cvratione tertianae stabilitur: / falsa impugnatur: / liberantvr Hispani medici a calumniis / a Doctore Pedro Barba.* Although printed without indication of the place or date of publication, Barba's work, it has been established, was published either in Louvain or Brussels in December 1641 or January 1642. Already as far back as 1905, in his critical survey of the early history of Cinchona,[1] a remarkable work for its documentation, accuracy and attention to detail, the Jesuit Father Joseph Rompel, Professor at the Stella Matutina, Feldkirch, definitely discredited the claim that the *Vera Praxis* was the first work to contain an account of Cinchona in Europe.

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[1] Santo Thomás, Domingo de, op. cit.

[2] Jussieu, Joseph de, *Description de l'Arbre a Quinquina.* La Société du Traitement des Quinquinas, M. Pancier, editeur (Paris, 1936).

[3] The great majority of well-informed historians are inclined to believe that Jussieu only reached Loxa in 1739.

[4] Jussieu, Joseph de, op. cit. French text, Appendix (14).

[5] Chifflet, Jean Jacques, *Pvlvis Febrifvgvs Orbis Americani ventilatus* (Bruxellae, 1653).

[6] Colmenero, Dr Don Joseph, *Reprobacion del Pernicioso Abuso de los Polvos de la Corteza de Qvarango, o China China, &c.* (Salamanca, 1697).

[7] Bergen, Heinrich von, *Versuch einer Monographie der China* (Hamburg, 1826), in *The Edinburgh Medical and Surgical Journal* (1827), vol. XXVII, p. 120.

We have also carefully searched Barba's work for any reference to '*Quina-Quina*' or '*China-China*', we have not found any. His method of combating fevers, in fact, was the old Galenic one, that of checking the fever by trying to 'free the patient of his corrupt humours', by means of purgatives and blood-letting. Moreover, an attentive examination we have carried out of the two controversial works which were specifically written condemning Barba's treatment of fevers, one by Plempius,[2] the other by Erich Mohy,[3] has been similarly fruitless. Indeed, the *Vera Praxis &c.* was not itself the cause of this controversy, but was Barba's own reply to an attack made against him by Martin Soers.

As physician to the Cardinal-Infant Ferdinand, governor of the Low Countries, Barba had just attended this Prince for malarial fevers: while under his treatment, His Serene Highness died. Two weeks later, on 26 November 1641, under the title *Adsertio Thesivm de Tertiana, &c.*, Martin Soers presented a thesis to the University of Louvain for the Medical Licentiate. This thesis was disputed under the Presidency of Plempius. Therefore, if it was not directly inspired by him, it must have been prepared under his guidance and supervision. In this work, Barba was quite openly charged with responsibility for the death of the Cardinal-Infant who, it was suggested, had died, not from fever, but from the repeated and excessive blood-letting to which Barba had subjected him.

It is worth quoting here, from Soer's Thesis, Conclusions VIII and X, in which he makes the charge that Barba, who is referred to as 'Iberus Medicus', 'kills the sick, and not only in Spain but also in these Provinces', and that he is 'unworthy of the name of a medical man and therefore ought to be struck off from the Register of Physicians':

> Conclusion VIII:...Wherefore he who follows the practice of Iberian doctors in intermittent tertian fevers, and when no plethora is present, once and again and more often by emptying of throbbing arteries...he acts against all reason and authority and experience; he kills [the patient]; and this as much in Iberia itself as in these Provinces.[4]
>
> Conclusion X:...He therefore who in such a case in place of these [principles?] supplies unboiled water cooled with snow and ice, melons, fresh plums, eatables [food] very liable to putrefaction and corruption, similarly refrigerated—he is unworthy of the name of medical man, and therefore ought to be struck off from the Register of Physicians, and be included among the corpse-bearers together with the Devil.[4]

In the light of these facts, therefore, it is not only out of question that Barba's work does not mention Cinchona at all, but that the assertion of Aristides A. Moll in the sense that 'a royal battle on the virtues of the drug long raged, as between P. Barba, Philip IV's physician (1642), and Colmenara [*sic*] in Spain,...'[5] and that of Dr Paredes-Borja that 'the physician Colmenero attacked Pedro Barba in his Reprobation of the abuse of the China China Powders',[6] have no justification whatsoever. Indeed, Dr José Colmenero's book[1] does not make the slightest allusion to Barba or his work, and it was published forty-five years later, that is to say, in 1697.

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[1] Rompel, Josef, op. cit.

[2] Plempius, Vopiscus Fortunatus, *Animadversio in Veram Praxim Curandae Tertianae Propositam a Doctore Petro Barba* (Lovaniae, 1642).

[3] Mohy, Erich, *Tertianae Crisis: qua DD Petri Barbae Protomedici praxis curandae Tertianae &c.* Bruxellae, 1642).

[4] Soers, Martin, op. cit. Latin texts, Appendix (15).

[5] Moll, Aristides A., op. cit. pp. 188–9.

[6] Paredes-Borja, Dr Virgilio, op. cit. p. 218.

Rompel, who in this is followed by Haggis and Norman Taylor,[2] thought he had discovered the first printed reference to Cinchona in Europe in a work by the Belgian physician Herman van der Heyden. Published with a dedication to the 'Grand-bailly', the 'Premier' and the 'Magistrat' of the city of Ghent, where it appeared in 1643, with a supplement in 1645, van der Heyden's book—*Discours et advis sur les flus de ventre douloureux, &c.*[3]—is now extremely rare. Rompel obtained it from the Library of the University of Louvain. The Wellcome Historical Medical Museum of London possesses a copy. In chapter II of the Sixth Discourse, which deals with tertian fevers, a reference is to be found to 'the powder which is here called *Pulvis indicus*'. By this name, it is a well-known fact, Cinchona was first often designated, particularly in northern and central Europe:

> ...If he [the patient] prefers, the powders alone, more or less the weight of one drachma of the above-mentioned species Diacarthami is here convenient, as even better the same quantity of the powder which is here called Puluis indicus.[4]

After a close study of the circumstances in which this reference was made, we have come to the conclusion that van der Heyden's *Pulius indicus* is not Cinchona. We base our opinion on three reasons. In the first place, it seems quite strange that at this early date the bark should have first become commonly known in Belgium,[5] rather than in Spain, where doubtless it first arrived. Secondly, van der Heyden was practising in Ghent and his book was published in that city, so that it must have been in Ghent or the corresponding province that the powder to which he refers was called '*Puluis indicus*'. Actually, as we shall see, there is extant a contemporary pharmacopoeia, issued in the same city of Ghent, the *Antidotarivm Gandavense*, in which the 'Pulvis indicus' is described: among its various constituents there is no mention of Cinchona under any of its designations of the time. Our third reason is the evidence given in this matter by Roland Sturm, a compatriot and fellow citizen of van der Heyden. In his book *Febrifugi Peruviani Vindicarum, &c.*, published in 1659, Sturm advocates dropping the name of *Pulvis indicus* for the Peruvian Bark in order to avoid the confusion between the Eastern and the Western *Pulvis indicus*:

> Most people however in this Belgium of ours call it '*Pulvis indicus*', as meaning something brought to us from the Indies: but this is too general a name, since several kinds of 'Pulvis' are brought from the Indies; and it does not distinguish whether it comes from the East or from the West Indies.[6]

Sturm, moreover, was completely successful in his initiative: from that time onwards, the name *Pulvis indicus* almost ceased to be used for Cinchona. It appears then, that there was at least one Eastern 'Pulvis indicus' which could be giving rise to confusion. And in our opinion it was this latter powder to which van der Heyden was referring.

If we are to rule out van der Heyden's work, and not taking into account such works as the *Antidotarium Bononiense* and the *Thesaurus* of Francisco Hernández,[1] *Protomédico de las Indias*, physician to Philip II and the first botanist to study the flora of Mexico, in which the '*China*' mentioned, as conclusively established by Rompel, definitely implies the '*China Radix' or 'Smylax China*' of the Linnaean classification,[2] or that of Pietro Castelli (1654), whose '*Quina*' or '*Pepitas de Quina*' allude to the Peruvian Balsam Tree, what, then, was the first printed European document to refer to Cinchona? Undoubtedly, until specific proof to the contrary is produced, the *Schedula Romana* should be accepted as this document. This ordinance's authorship has been attributed to Pietro Paolo Puccerini, apothecary of the Pharmacy of the Collegio Romano, and apparently there were two editions of it, the first printed in 1649, the second in 1651. It is a mere leaflet containing instructions for the use of Cinchona, resembling the instructional leaflets which accompany patent medicines to-day: in the same way, the Roman apothecaries of the time distributed the *Schedula* with samples of the bark. These instructions, written in Italian and translated into English, read as follows:

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[1] Colmenero, Dr José, op. cit.

[2] Taylor, Norman, 'Cinchona in Java', *The Story of Quinine* (New York, 1945), p. 31.

[3] *Discours et advis / sur les flus de ventre douloureux, / Soit qu'il y ayt du sang ou point. / Sur le Trousse gallant : dict Cholera morbus : la peste : les effets signalés et incroyables de l'eau....Composés par M. Herman van der Heyden, / Médecin Pensionaire de la ville de Gand. / Imprimé a Gand, chez Seruais Manilius, au Pigeon / blanc,* M. DC / XLIII. *Et l'addition :* M. DC. XLV.

[4] Heyden, Herman van der, op. cit. *Sixième Discours. / Sur les Fieures Tierce, & Quarte, &c.* Chapitre II, 'De la Fieure Tierce', p. 97. French text, Appendix (16).

[5] It is demonstrated that Michael Belga, [Bolag] physician to the Marquis de Mancera, successor to the Count of Chinchón as Viceroy of Peru, was not able to take it back with him to Belgium earlier than 1649, as the Marquis de Mancera only surrendered office and left Peru in September 1648.

[6] Sturm, Roland, op. cit. Sectio Prima, p. 8. Latin text, Appendix (17).

Instructions for the Use
of the Bark called
Fever Bark

This Bark is imported from the Kingdom of Peru, and is called China, or better *China Febris*, and is used against quartan and tertian fevers, accompanied by shivers: it is used as follows:

Two 'dragmae' of finely ground and sieved Bark to be mixed in a glass of strong white wine three hours before the fever is due; and as soon as the shivers begin, or the first symptoms are noted, the patient is made to drink the whole infusion thus prepared, and put to bed.

It is to be noted, that in the event of tertian fever this bark can be administered, as stated above, when the fever has persisted for many days.

The constant use of this remedy has cured practically all the patients who have taken it, having at first well cleared the bowels. For four days after no other medicine whatsoever must be taken. It must be used only on the advice of the Physicians, who may consider whether it is timely and appropriate to administer it.[3]

The second printed reference in Europe to Cinchona is of a more substantial nature, being Chifflet's subtle attack on the bark, *Pvlvis Febrifvgvs Orbis Americani ventilatvs*, published in 1653. A defence of its use in the *Pvlvis Pervvianvs Vindicatvs de Ventilatore &c.*, by Father Honoré Fabri (Antimus Conygius), appeared two years later.

When we come to investigate the first printed reference to Cinchona in any English work we find that an unwarranted and inaccurate statement by Howard W. Haggard may have misled many into believing—once more the error induced through second- or third-hand reference—that it was much earlier than was really the case. In his popular account of the history of medicine, *The Doctor in History*,[4] Haggard states: 'In 1618, the first *London Pharmacopoeia* appeared...There were nearly two thousand remedies described in this book, the vast majority of which were herb medicaments. A few of the remedies were valuable beyond question and are in use to-day: there was quinine, the great medical discovery of the seventeenth century....' Quinine, of course, was not then discovered and even Cinchona had not reached Europe at that early date. In fact, the bark's first appearance in the *Pharmacopoeia Londinensis* is in the third edition of 1677, where it is listed in the group headed '*Cortex*' as '*Cortex peruanus*' (p. 4). We have searched through the various editions which were published between 1618 and 1677 (1639, 1650, 1662): in none of these is Cinchona to be found under any of the synonyms by which it was known. It figures again in the edition of 1721, under the title '*China Chinae*', with the sub-title '*Quinquina Cortex Peruanus & Peruvianus*'.

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[1] Hernández, Francisco, *Rerum medicarum novae Hispaniae thesaurus seu plantarum, animalium, mineralium*...(Romae, 1651).

[2] Plant whose rootstock, after Caius had advocated it, especially against the 'suette miliaire', was very much in favour at the end of the sixteenth and first half of the seventeenth centuries.

[3] Sturm, Roland, op. cit. p. 146. Italian text, Appendix (18).

[4] Yale University Press (1934), p. 268.

However, what appears to be the first written mention in English of the use of Cinchona is to be found in an entry in the Case-Book of John Metford of Northampton, entitled *Observationes et Curationes*,[1] which he started keeping in 1652: a pregnant woman suffering from quartan fever and with '*paroxysmis violandissimi gravissimi*' was cured with small doses of the Jesuits' Bark in 1656.

In England, the first known advertisement of the bark was printed in the weekly news-sheet *Mercurius Politicus* in 1658. This advertisement appeared four times (1 and 29 July; 28 October and 16 December), and reads as follows:

> These are to give notice, That the excellent Powder known by the name of the Jesuit's Powder, which cureth all manner of Agues, Quotidian, Tertian and Quartan, brought over by James Tompson Merchant of Antwerp, is to be had at the Black-Spred-Eagle over against Black and white Court in the Old Baily, or at the shop of Mr. John Crook, at the sign of the Ship in St. Pauls Churchyard, a Bookseller, with directions for using of the same.[2]

In the last issue of the advertisement was added to its text the following testification:

> ...Which Bark or Powder is attested to be perfectly true by Doctor Prudjean and other eminent Doctors and Physicians who have made experience of it.[3]

Dr Prudjean seems to have been Sir Francis Prujean, a physician of great repute at the time and President of the Royal College of Physicians of London from 1650 to 1653.

The first work by an English physician to refer to Cinchona was published in 1660 by Thomas Willis.[4] Less than twenty years later, in 1676, as is well known, Thomas Sydenham had acquired such experience in the use of the '*Febrifugum Peruvianum*', that he was considered an authority on it. He spoke and wrote of it with complete confidence; 'the Peruvian Bark' had come to constitute his '*Sheet Anchor*'.

Before we leave this question of literary priorities it seems worth drawing attention to the earliest known illustrations of the Cinchona tree. The first illustration ever published in Europe appeared in 1661 in the work of the distinguished and prolific Danish medical writer, Thomas Bartholinus, *Historiarum Anatomicarum, & Medicarum Rariorum, Centuria V & VI*. Bartholinus informs us that he had received the drawing he reproduced there, a complete view of the tree (Plate **17**, fig. 1), from Hieronymus Badus (Bardi), transmitted through their common friend Heinrich von Moinichen. We know that Badus, who maintained a correspondence with all the great physicians of his time, also sent drawings of the tree to Severino, Castelli, Moreau and others. It has not been possible for us to consult all the works of these authors—some of them are very rare and difficult to find—but we have found no indication that any of them anticipated Bartholinus.

In the following year, 1662, for the second time, a very similar although not identical view of the tree was published in John Jonston's *Dendrographias: sive Historiae naturalis de arboribus et fructibus...libri X* (Plate **17**, fig. 2). The preface of this work is dated 1661, but Jonston certainly knew that of Bartholinus, for he refers to it in his account of the 'Arbor febrifugus Peruvianus' (p. 476). Of Scottish parentage but born in Poland, Jonston was a celebrated naturalist and physician; he had studied and practised in Scotland, London, and practically every country in Europe. Among Jonston's wide circle of friends and acquaintances was Pietro Castelli, who wrote the account of the Civet for his *Theatrum Historiae Naturale* (1650–3). It is not impossible that Jonston, who had been collecting materials and illustrations for his botanical work for some years, had seen and copied the drawing which Badus had sent to Castelli.

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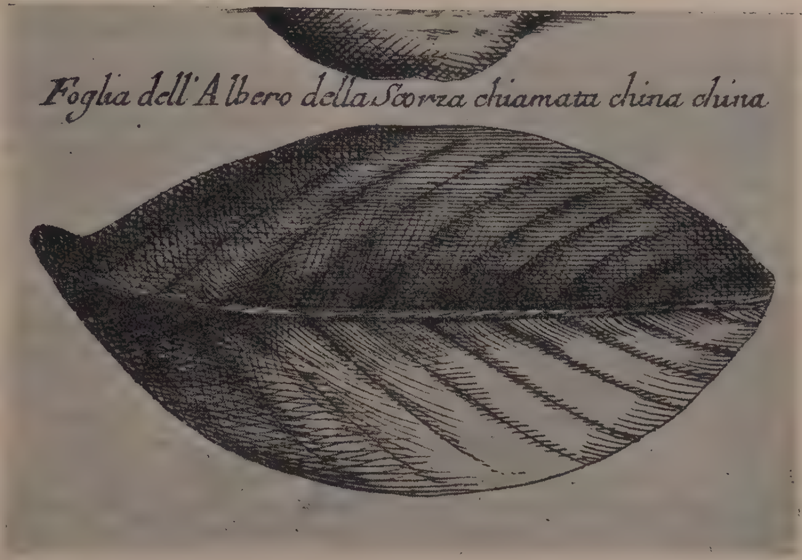
[1] Metford, John, *Observationes et Curationes Northamptoniae absoluta; incipiendo ab anno salutis Christiana* 1652. MS. Sloane Collection no. 2812, British Museum, p. 134.

[2] Photographic reproduction in E. M. Holmes, '300 Years of Cinchona'. *The Chemist and Druggist* (December 1930).

[3] Quoted in Sir Humphrey Rolleston, op. cit.

[4] Willis, Thomas, *Diatribae duae medico-philosophicae...altera de febribus...*(Londini, 1660).

The third illustration of Cinchona published in Europe, shows only the leaf of the tree. It appears in Francesco Redi's *Esperienze, &c.*,[1] published in 1671. Its legend reads as follows: *Leaf from the Tree of the bark called china china.*[2] (Text-fig **1**).


Foglia dell'Albero della Scorza chiamata china china

Text-fig. 1. 'Leaf from the Tree of the Bark called china china', in Redi's work *Esperienze intorno a diverse Cose Naturale, e particolarmente a quelle, che ci vengon portate dall' Indie*, published in 1671, the third illustration to be published in Europe relating to the Cinchona Tree. (Courtesy of the General Library, British Museum (Natural History).)

VII. Early controversy about the medicinal value of Cinchona

If, without any reserve, the discovery of Cinchona was an incalculable benefit for humanity, it does not follow that its merits were immediately and universally recognized. On the contrary. Although it may appear strange to-day, from the dawn of its introduction into Europe, after the publication of the *Schedula Romana*, a bitter controversy regarding its virtues raged between the various schools and practitioners for half a century or more. Yet, only when the historical conditions predominant in that epoch are studied, can that singular fact be explained. One of the chief factors in this dispute was religious intolerance, for many Protestants carried their hatred of the Roman Church, and particularly of the Jesuits, to such a point as to condemn *a priori* a remedy which the efforts of the Jesuits had made available to sick humanity in Europe.

The leading figures in this controversy were Ioannes Iacobus Chiffletus (Chifflet), physician to the Archduke Leopold of Austria, Regent of Belgium and Burgundy,[3] who wrote against the bark; the Jesuit Father Honoratus Faber (Fabri), who, under the pseudonym of *Antimus Conygius*, championed the bark against the attacks of Chifflet and Renatus Moraeus (Moreau), Professor of Medicine in the Sorbonne and physician to the King of France; Vopiscus Fortunatus Plempius (Plemp), 'Rector Magnificus' of

[1] *Opere di Francesco Redi*, op. cit.

[2] *Foglia dell' Albero della Scorza chiamata china china, Tauola 5.*

[3] Archduke Leopold was himself attacked by malarial fevers. Chifflet administered to his august patient the powders of the bark (*Peruviani Pulveres*), but discontinued its use at the Archduke's request, who abhorred its bitter taste (*Ó quam est amarus!* he exclaimed), whereupon the prince suffered a relapse. This unfortunate occurrence was blamed on the bark.

the University of Louvain, and Professor of Medicine in it, writing against Fabri under the name of *Melippus Protimus*; Badus, Sturm and Brunacius who entered the lists against Chifflet and Plemp; while in England, Gideon Harvey poured scorn on Sir Robert Talbor, his claims as 'pyretiatro' and his 'method' of treating them: the 'Jesuits' Bark'.

Ignorance of and inexperience in the use of the bark, the unequal quality of the various consignments of bark which arrived in Europe at that time, the confusion which reigned concerning its correct identification, all these factors contributed powerfully to keeping alight the controversy referred to. The effect of this state of affairs on the reputation of Cinchona was, as much later it was put by a famous Colombian, Don Francisco Antonio Zea,[1] the first Colombian Minister to Great Britain, 'its alternating epochs of depression and glory'. Relevant to this is that, if in 1655, Moreau wrote from Paris to a friend in Brussels (Plemp) '...the reputation of the Peruvian powder is so dead in this city that it is no longer mentioned and we no longer prescribe it',[2] in 1702, the celebrated Italian clinician Bernardino Ramazzini in a university lecture declared that 'surely after the use of this remedy has become known...it must be avowed that, concerning the doctrine of fevers and the method of curing them, a change (revolution) has been made comparable to that which all know followed, in military affairs, the invention of gunpowder'.[3]

The extraordinary career of Sir Robert Talbor[4] the 'charlatan of Essex' (1639–81), still the subject of opposing views, and which had such an adverse effect on the prestige of the physicians of his day, unquestionably must be recognized as one of the most influential factors in the introduction of Cinchona into the pharmacopoeia. As will be remembered, by means of his 'marvellous secret', the *arcanum*, known to the French as 'le remède de l'Anglais', from his position as simple 'Apothecary's man', as Sydenham referred to him, Talbor attained the highest social and professional distinction to which a physician could aspire. Appointed personal physician to Charles II of England, Louis XIV of France and Marie-Louise of Orleans, wife of Charles II of Spain, he was knighted by the kings of France and England and made a Fellow-Commoner of St John's College, Cambridge. In order that his subjects might benefit from his 'secret', Louis XIV also paid him 2000 *louis d'or* and an annual pension of £2000 for his prescription. Talbor's 'marvellous secret', revealed at his death, did not turn out to be anything else than the discredited Cinchona.

From the point of view of medical ethics, Talbor's general behaviour cannot be excused. At the same time we must acknowledge that he must have been a man of great natural gifts, brilliant intelligence and singular personal charm.

VIII. SOME ANTECEDENTS ON THE BOTANICAL CLASSIFICATION OF CINCHONA

It was Linnaeus who, then as now regarded as one of the greatest naturalists of all time, in 1742, established the classification of the 'Quina' tree, giving to the genus the name *Cinchona*. He based his classification upon the drawing of the leaves, flowers and fruit of the tree (Plate **18**) made by La Condamine in Cajanuma, two and a half leagues south of Loja (Plate **19**), in February 1737, and upon his accompanying description.

On the occasion of the 'Cinchona Tercentenary'—celebrated in London and the United States in 1930, to commemorate the first recognized use of Cinchona by the

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[1] Zea, Francisco Antonio, 'Memoria sobre la quina según los principios del Sr. Mutis'. *Anal. Hist. Nat.* (Madrid, 1800), vol. II, pp. 196–235.

[2] Conygio, Antimo, *Pervviani Pvlveris Febrifvgi Defensor Repvlsvs a Melippo Protimo Belga* (1665), p. 4. French text, Appendix (19).

[3] Ramazzini, Bernardino: *Orationes Jatrici Argumenti &c.* Patavii. M. DCC. VIII. *Oratio Tertia: Veram Febrium Theoriam & Praxim inter ea, quae af huc desiderantur esse recensendam. Habita die 6. Novembris* M. DCC. II, p. 102. Latin text, Appendix (20).

[4] The name is often given as *Tabor*: it is so spelled in Linnaeus, plate I (q.v.). There are to-day many Tabors in Essex and they trace back two to three centuries. While in France, Talbor changed his name to *Talbot*.

Europeans (case of the Corregidor of Loxa)—statements were made[1] in the sense that the first person to suggest the name 'Cinchona' appears to have been Sebastiano Bado, and that this had been accepted and confirmed by the Communal Council of Ghent. This body was responsible for the regulations governing medical and pharmaceutical practice in Flanders and supervised the admission of new candidates into these professions, receiving their 'oaths', in accordance with the resolutions of the *Collegium Medicum*. Nowhere in Bado's work have we found any support for this statement. Moreover, in response to our inquiries, Prof. Ruyssens, the Rector, and Prof. Apers, the Librarian of the University of Ghent, have made in that respect a careful search in the *Antidotarivm Gandavense*: the name Cinchona does not appear in it. This was the official pharmacopoeia used in Ghent and it was completed in 1690. In the earlier edition of 1663, however, an entry appears which may have given rise to some confusion. In the section devoted to powders[2] there is a reference to '*Pulvis indicus, sive Catholicus, Auttore Marco Cornacchino*': nevertheless, the formula of this powder is given in detail[3] in the *Antidotarivm* and it does not include Cinchona.

In these circumstances, and as far as our investigations have revealed, the first official Pharmacopoeia to include Cinchona among the official remedies was the *Pharmacopoeia Londinensis* of 1677, referred to on p. 297, where it appeared with the name 'Cortex Peruanus'.

This first classification of Linnaeus, made just in time to be included as the last of the 'Addenda' which follow the 'Appendix' in his *Genera Plantarum* of 1742, was by no means definitive. Indeed, it could not be so, for the learned Swede had never seen the plant for himself and La Condamine's *Memoir* and drawings lacked certain data which were essential for the establishment of all the characters of the genus. In his subsequent works, Linnaeus continued to develop his description. In his *Materia Medica* (1749) he added some pharmaceutical particulars, and in the *Species Plantarum* (1753) he first gave to the 'Quinquina Condamin' the specific epithet '*officinalis*'.

The Spanish Government, meanwhile, had sent to Loxa Don Miguel de Santisteban, Director of the Upper Mint of Santa Fé (New Granada, Colombia), with instructions to organize locally the trade in the bark (Cabildo de la Quina).[4] Back in Bogotá, Santisteban presented samples and a beautiful coloured drawing of the tree to the learned philosopher, mathematician and naturalist Don José Celestino Mutis, who, in turn, sent them to Linnaeus, in 1764 (Plate **20**). Upon these, Linnaeus supplemented his classification. The consequence was that, as they represented the variety *Palo de Requeson*, *Yellow Bark* or *Cinchona cordifolia*, whereas the drawing and description of La Condamine depicted the *Cascarilla fina*, *Cascarilla de Uritusinga* or *Cinchona lancifolia*, in the far more detailed description included in the twelfth edition of his *Systema Naturae* of 1767, *Cinchona officinalis* no longer represents the variety drawn by La Condamine (*C. lancifolia*) but that of Santisteban and Mutis (*C. cordifolia*). In his *Supplementum Plantarum* the younger Linnaeus perfected the description of the genus *Cinchona* with new information and samples provided also by Mutis.

Two extracts from the Latin correspondence which passed between Mutis and Linnaeus,

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[1] Dock, George, 'The Medicinal Use of Cinchona'. In *Proceedings of the Celebrations of the Three Hundredth Anniversary of the First Recognised Use of Cinchona. St Louis Mo.* (1931), p. 157.

[2] Tractatus XI, de pulvis simplicibus, & solutivis, p. 134.

[3] ℞

Scammoneae per sulphur, praeparatae	℥j
Antimonii praeparati ut dicetur	℥vj
Crystalli tartari	℥iiij

Misce fiat pulvis.

[4] *Relación informativa práctica de la quina de la ciudad de Loxa y demas territorios donde se cria... segun demostracion que hizo el año de 1753 Dn. Miguel de Santisteban, para que se plantificase, conduciéndola por los parages y puertos que cita, á España, con igual cuenta del costo hasta almacenarla.* Santa Fé, 4 de junio de 1753. Biblioteca de Palacio, Madrid, *Miscelánea de Ayla*, MS. no. 2823, Tomo VIII, pp. 82–8.

which resulted in the latter's definitive classification of the genus *Cinchona*, are worth recording here. We quote Mutis's letter from the English translation published by Si James Edward Smith, first President of the Linnean Society, in the volume devoted to the correspondence of Linnaeus;[1] and Linnaeus's letter from Dr Blanco-Juste.[2]

In his letter to Linnaeus, dated in Santa Fé de Bogotá 24 September 1764, Mutis writes

> ...But that my present letter may not seem entirely unprofitable, I send you a drawing with some of the flowers, of the Peruvian Bark. I am not certain whether the celebrated Monsieur de la Condamine has given any drawing along with his description, nor whether you had an opportunity of examining a dried specimen, as I find no mark indicative of this in the generic description of Cinchona, in your Stockholm edition of 1754....

In his reply to Mutis, Linnaeus says:

> ...I received in due time, eight days ago, your letter dated the 24th day of September o 1764, and was greatly moved and overjoyed by it, as it contained a beautiful drawing of the quina bark, together with the leaves and flowers, which flowers, never seen by me until now really have given me an idea of a very rare genus, and very different from that which I acquired through the figure of Monsieur Condamine. I am very grateful for everything...[3]

IX. Final words

The varieties of Cinchona known at present exceed 150, and since the plant is heterostylous, a natural characteristic which prevents autopollination and conduces to hybridism, their number tends to increase indefinitely. It was this fact, not then clearly established, which was mainly responsible for the long, acrimonious and generally futile controversies in which some eminent naturalists engaged for many years, regarding the botanical characteristics of this or that species or variety of Cinchona. Arguing from the inspection of different samples, they were attempting to define characteristics which were changing, even within their lifetime.

Foremost among the botanists and naturalists who contributed to the study of the Ecuadorean, Peruvian and Bolivian quinologies were Hipólito Ruiz, José Antonio Pavón, Juan Tafalla and Juan Manzanilla; of that of New Granada (Colombia), José Celestino Mutis (Plate **21**), Francisco José de Caldas, Fray Diego García, Francisco Antonio Zea, José Joaquín Triana and Nicolás Osorio. Thanks to the discoveries of Cinchona to the north of the equator by Santisteban, Sebastián José López Ruiz, Mutis and García, the bark which until then had to make the long circuitous journey around Cape Horn to reach Europe, to the great disadvantage of its condition, was now sent directly across the Atlantic, from the port of Cartagena, a circumstance which greatly reflected at the time not only upon the commercial aspects of the bark, but consequently upon its medical implications. Great and learned contributions to our present knowledge of the plant were made by various distinguished European naturalists and botanists: among them the most outstanding were Joseph de Jussieu, Jacquin, Humboldt, Bonpland, Kunth, Karsten, Laubert, Weddell, Delondre, Pöppig, Swartz, Wahl, Spruce, Lambert, Markham, etc.

The beautiful Cinchona plantations of Java, which, before the war, supplied the bark from which 85 to 90% of the world consumption of quinine was extracted, a yearly average of 750 tons, were developed from the seeds of *Cinchona calisaya* collected for Charles Ledger in the year 1864 in the Yungas of the Department of La Paz, in the region of Chulumani, near the River Beni (tributary of the Upper Amazon), by the Indian Manuel Icamanahí (Norman Taylor, wrongly, refers to him as Manuel Incra Mamani).

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[1] Smith, Sir James Edward, *Selection of the Correspondence of Linnaeus and other Naturalists from the Original Manuscripts* (1821), vol. II.

[2] Blanco-Juste, Dr Francisco J., *Historia del Descubrimiento de la Quina* (Madrid, 1934).

[3] Spanish text, Appendix (21).

This action of Manuel Icamanahí cost him his life. Humanity, it may be added, owes him the belated honour of a memorial, for his seeds were the source of the quinine which has been used almost everywhere for nearly a century, not only against malaria, but in the treatment of influenzal, cardiac and other affections. As it should also acknowledge its immense debt to Charles Ledger, who wandered for years looking for those seeds, and to the distinguished agronomist and arboriculturist L. C. Bernelot Moenz, Director of the Government Cinchona Plantations of the Netherlands East Indies. With great skill, perseverance and insight, the latter carried out an exhaustive series of experiments, particularly by means of grafts, in order to select, cultivate and improve a plant with a high alkaloid yield: the result, as we all know, is the *Cinchona ledgeriana*, which is now grown throughout the plantations of that island.

X. APPENDIX

Original texts

(1) Bado, Sebastiano, *Anastasis Corticis Pervviae, Sev China Chinae Defensio* (Genvae, 1663), ch. II, pp. 21–2:

Capvt II

De Arboris Cortiferae antiquitate, & quomodo recens innotuerit

...Redeo ad Historicam *Bolli* narrationem, narrantis in cit. Epistola, iam olim *Indis* hominibus innotuisse Corticem, sibique in morbis illum adhibuisse; at conatos semper fuisse omni ope, ne *Hispanis* hominibus innotesceret Remedium, quibus potissimum, & Europaeis insensi sunt.

(2) Bado, Sebastiano, op. cit. ch. I, p. 19:

Subditque rursum *Bollus*, apud *Indos* corticem vsurpari promiscué, in omni febre. Modus quo exhibent corticem *Indi*, nil descrepat a nostro;...

(3) *Opere di Francesco Redi.* In Venezia, Scritta Dall' Abate Salvino Salvini, 1771. Vol. II, pp. 69–70.

Sono ancora da farsi nuove esperienze intorno alla radice di *Calumba*, creduta un grandissimo alessifarmaco; intorno alle Vainiglie, ed intorno al legno di Laor, e di Solor, i quali essendo molto amari, parrebe ragionevoli, che veramente avessero tutte quelle singolari prerogative, che dagli Scrittori son loro attribuite, ma in fatti non se vederle con evidenti, como evidentissimi veggio sempre gli effetti della maravigliosa scorza di quell' albero Peruano de' monti di Guajachil, la quale scorza chiamata volgarmente *China China*, e dagli Spagnuoli *Cascarilla de la oja*, si usa per interrompere e per debellar gl' insulti delle febbri quartane, e delle terzane semplici, doppie, e continue. Ed in cio grandissimo obbligo porta tutto il nostro Mondo a quei Padri della vostra venerabilissima Compagnia i quali prima di ogni altro, con tanta loro gloria, la portarono in Europa.

(4) Bado, Sebastiano, op. cit. Cap. XXIII, p. 240:

Io infrascritto so piena, & indubitada fede,...poiche di piú dico, che dall' ano 1647, sino al presente, che á me mi á stata mandata dal Perú, habbi fatto miracoli per cosi dire....Si che questo e quanto deuo di ció far fede per la veritá, & per l' esperienza, essendoui presso anche l' Eminentiss. & Reuerendiss. Sig. Cardinale de Lugo della nostra Compagnia una gran Cassa di fedi, che testificano poter darsi questa Corteccis á tutti, per l' effetti osseruati, che tutti han guarito. Et in fede hó fatto la presente di mia mano sottoscritta, e con il sigillo della Spetiaria nostra sigillata. In Roma 5. Aprile 1659.

Locus Sigilli.

Petri Pauli Puccerini della Compagnia di Giesú, Spetiale del Collegio Romano.

(5) Vázquez de Espinosa, Fray Antonio, *Compendio y Descripcion de las India Occidentales.* MS. in the Vatican Library (Barberini Collection No. 3584), Segunda Parte Libro V°:

Cap. 26. En que prosigue la descripcion del distrito de esta ciudad [Chuquisaca o Villa d la Plata: hoy Sucre, la antigua capital de Bolivia], y en particular de la calidad de los arbole y sus maderas.

De todos los arboles referidos en el capitulo precedente, solos la palma cria cocos, el noga nueces muy encarceladas, el algarrobo algarrobas como las de España, aunque se diferencia en ser blancas y mas dulces. . .el arbol de la quinaquina cria tambien otras vaynas a modo d las algarrobas; los demas arboles no dan fruto.

. . . .

Del arbol quinaquina se saca una resina de color de higado muy odorifera y saludable, co su sahumerio se consuman frialdades y reumas de caueça, con esta resina mezclada con aceit se curan heridas, y llagas, y el mismo efecto tiene el aceite que se saca de sus pepitas y es co mas eficacia: el arbol quinaquina es muy hermoso y su madera muy odorifera, y fuerte, e color de su madera blanco y leonado a vetas.

(6) Cobo, Bernabé, *Historia del Nuevo Mundo*, Lib. VI, Cap. LXXXI, p. 88:

Quina-Quina llaman en el Perú a un árbol grande y hermoso como un mediano olivo; la hoja del tamaño y talle que la del limón ceuti; el tronco es algo colorado, resinoso y aromático. Es árbol caliente en el segundo grado, estíptico y seco y de suave olor. Echa unas pepitas por semilla del tamaño de almendras, de color amarillo y de sustancia oleaginosa, que co fragancia huelen amigablemente, son asinismo calientes y estípticas en el segundo grado, y secas en más del primero. Sajando el tronco y ramas destila una resina olorosa, que s congela tanto, que se muele en polvos y queda de color negro claro, la cual es caliente y más seca que las pepitas. Nace este árbol en la tierra caliente de la provincia de los Charcas en e Perú. Si con su corteza se limpia de ordinario la dentadura, la aprieta y la conforta; y el palo raspado y cocido con Polipodio, hojas de Sen y anis, y el cocimiento tomado en ayunas algunas mañanas, desopila el estómago, higado y bazo, mundifica y limpia la vejiga. Las hojas majadas y puestas sobre las heridas frescas, las desecan y juntan, y el cocimiento dellas con salmuera, hojas de *Chilca* y *Molle* deshincha las piernas gotosas. De las pepitas de este árbol se hace un aceite maravilloso para toda herida fresca, el cual se usa mucho en Potosí. . . .

(7) Monardes, Dr Don Nicolás, *Historia Medicinal de las Cosas que se traen de nuestras Indias Occidentales que sirven en Medicina.* (Sevilla, 1574):

Muy Magnifico Señor,
Y Muy Nombrado Doctor.

. . . . . .

Assi mismo embio á v.m. un fructo de un arbol, que es de grandes provechos, y estos arboles no se hallan en otra tierra sino en esta, es del tamaño de una Enzina de las de Castilla, tiene la corteza como Mesto, y la hoja como Fresno: tiene muchas virtudes, porque la corteza hecha polvos, y echados en qualquiera llaga, que aya menester lipmiarla, por estar suzia, la limpia, y despues haze crecer la carne, y la sana muy bien. Fregando los dientes con estos polvos los limpia, y puestos en las enzias descarnadas las encarna, y aprieta los dientes que se andan. Coziendo las hojas deste arbol bien en agua, y lavando con el agua qualquier hinchazon, que tenga qualquier llaga, ó que este apostemada, quita la hinchazon y la apostema. Y poniendo unos pañitos mojados eneste cozimiento tibios, sobre la medicina que se pone sobre la llaga, ó sobre los polvos que de la corteza se hizieron, que se ponen para sanar las llagas, haze que las llagas sanen mas presto: haziendo que no venga humor á ellas. Del arbol sale una Resina olorosa que sirve para sahumar en muchos males de cabeça, y para hazer emplastos para muchos males, ay la embio á v.m. Del fructo hazen los Indios cierta bevida, que es para ellos muy saludable. v.m. los mande sembrar, que holgaria que maciessen, porque seria cosa de mucho contento, por los provechos que tiene en medicina, y por la novedad del arbol, porque en todo tiempo tiene muy lindo olor. . . .

. . . .

De Lima, en el Peru, á veynte y seys de Diziembre, del año de mil y quinientos y sessenta y ocho.

Besa las manos de v.m.
Pedro de Osma y de Xara y Zejo.

(8) Ruiz, Don Hipólito, *Relacion historica del Viage, que hizo á los Reynos del Perú y Chile el Botánico dn. Hipolito Ruiz en el año de 1777 hasta el de 1788, en cuya epoca regresó á Madrid.* MS. at theBotanical Department, British Museum (Natural History), fol. 65 (4):

Myroxylon peruiferum v. [vulgo] Quinoquino: árbol elevadisimo y frondoso, de tronco grueso, derecho, liso y ceniciento, como todas sus ramas. La corteza es de un blanco pagizo por la parte interior y segun la mayor ó menor cantidad de resina de que está penetrada es mas ó menos granugienta, compacta, y pesada y de color unas vezes rubicundo, otras cetrino y otras de un castaño obscuro, finalmente es en su olor y sabor aromatico-balsamicos, semejante al Balsamo rubio Peruviano que con el nombre de Balsamo blanco se vende en las Boticas y Droguerias. A la Resina que se recoge de los Quinoquinos llaman en el Perú *Estoraque*, usan de ella para sahumar los aposentos, como tembien de los Frutos, llamados Pepitas ó Semillas de Quinoquinos, los quales reducidos juntamente con las cortezas á polvos mezclan con sebo ó resinas y aplican en parches para mitigar los dolores de cabeza. Las hojas frescas machacadas sueldan las heridas recientes y lo mismo hace el Balsamo y corteza conocidos por admirables balsamicos y vulnerarios. De los frutos se hace el Aceyte llamado de Quinaquina: tomando quatro onzas de ellos bien contundidos, se infunden en un quartillo de vino por veinte y quatro horas, despues se cueze á fuego manso con libra y media de Aceyte comun hasta la sequedad, se añade entonces una libra de trementina y ultimamente onza y media de incienso y otro tanto de mirra. Dicen que este Balsamo hace maravillosos efectos en las llagas de los pechos, que aglutina y cura las ulceras y llagas, De los Troncos sacan los Indios maderos para pies derechos y los prefieren á los de otros árboles por su fortaleza y larga duracion. En los extremos de las ramas de los Quinoquinos, como mas apartadas del Tronco, hacen con mas frecuencia que en las de otros sus nidos los Paxaros Poccochycuys, Kcuychis ó Hediondos, para libertar á sus hijuelos ó huevos de los Monos y de otros animales que suben á los árboles en busca de alimento.

(9) Cobo, Bernabé, op. cit. Lib. VI, Cap. XCVII, p. 100:

Del árbol de calenturas

En los términos de la ciudad de Loja, diócesis de Quito, nace cierta casta de arboles grandes, que tienen la corteza como de canela, un poco más gruesa, y muy amarga; la cual, molida en polvos, se da á los que tienen calenturas y con sólo este remedio se quitan. Hanse de tomar estos polvos en cantidad del peso de dos reales en vino ó en cualquiera otro licor poco antes que dé el frio. Son ya tan conocidos y estimados estos polvos, no sólo en todas las Indias, sino en Europa, que con instancia los envían á pedir de Roma.

(10) Calancha, Fray Antonio de la, *Coronica Moralizada del Orden de San Avgvstin en el Perv.* (Concluded in Lima in 1633 and first published in Barcelona in 1638.) Lib. I, Cap. IX, p. 59:

Dase un arbol que llaman de Calenturas en tierra de Loja, con cuyas cortezas, de color de canela, echas polvos dados en bebida el peso de dos reales, quitan las calenturas i tercianas; an echo en Lima efectos milagrosos. Dase cañafistola en abundancia, çarçaparrilla,. . . la quinaquina remedio general (ya en pepitas, ya derretida en bollos) de varios males de cabeça y cuerpo, i de todas eridas; la quiuna semilla como la mostaça, aunque es blanca i no redonda, eficaz medicina contra molimientos de cuerpo, i peligros de pasmo; el pincopinco, remedio universal de varias enfermedades. . . .

(11) Ruiz, Don Hipólito, op. cit. Folio 24 (4): MS. at the Botanical Department, British Museum (Natural History):

Lliclias: Es un pedazo de paño ó bayeta ó de otra tela de vara en quadro, adornado con varias listas de diferentes colores; y algunas listadas con cintas de oro y plata y fransas de Tisú: Se las ponen sobre los hombros, prendiendolas hácia el pecho con un *Timpis*, que significa punzon ó cosa que asegura uniendo ó trabando, como si fuere un grande alfiler. . . .

(12) Cobo, Bernabé, op. cit. Lib. VI, Cap CXXVIII, p. 124:

De la Quínua

La Quínua es un árbol del tamaño de un Olivo y de ahí para abajo hasta no crecer más de un estado; tiene las ramas y tronco rojos, con la corteza muy delgada, que con facilidad se despide. . . . Es árbol tan fuerte en resistir el rigor del frio y heladas como el Quishuar; y asi, sólo estas dos castas de árboles nacen en los rigorosos páramos del Perú, especialmente en las provincias del Collao. Hacen de la Quínua muy buen carbón, que es bien necesario donde tanto frío hace.

(13) Ruiz, Don Hipólito, op. cit. Folio 35 (4):

Atravesando varios Ingenios y Lagunas, baxamos á la quebrada de la *Quinua* (nombre adquirido) por criarse en ella muchos árboles llamados *Quinuares* ó *Quinhuares*: los quales sirven de grande auxilio á los Mineros del Cerro de Yauricocha para los edificios e Ingenios por la fortaleza de sus troncos, y (por ser) la madera de mucha duración en el fuego. De este árbol establecimos el género *Polylepsis*, tomado el nombre de la multitud de capas delgadas a (ma)nera de vitelas de color melado, en que progresivamente se va desprendiendo su corteza á proporcion de los años que tiene.

(14) Jussieu, Joseph de, *Description de l'Arbre a Quinquina.* La Société du Traitement des Quinquinas. M. Pancier, editeur (Paris, 1936):

Ils l'appelaient *yara chucchu cara chucchu. Yara* signifie arbre, *cara* l'écorce, *chucchu* frisson de la fièvre, pour ainsi dire l'arbre de la fièvre intermittente. Ils l'appelaient aussi *ayac cara*, ce qui signifie écorce amère.

(15) Soers, Martin, *Adsertio Thesivm de Tertiana &c.* (Lovanii, 1642):

Conclvsio VIII (p. 3):

...Quapropter qui sequitur Iberorũ praxin Medicorũ in tertiana intermittente, nullaq́; plethorá praesente, semul interumq́; & saepiús venam tundentium in principio neglectá primae regionis evacuatione, contra omnem rationem agit & authoritatem & experientiam; aegrumq́; occidit: & id tam in Iberia ipsa, quam in hisce provinciis.

Conclvsio X (p. 4):

Qui ergo tali casu, loco horum praebet aquam crudam nive & glacie refrigeratum, melones, pruna recentia, edulia maximé putredini & corruptioni obnoxia, similiter frigefacta: indignus est Medici nomine ideoq́; ex Iatrorum albo eradendus, & vespillionibus adscribendus cum Diauolo.

(16) Heyden, Herman van der, *Discours et advis / sur les flus de ventre douloureux, / Soit qu'il y ayt du sang ou point./. . . Imprimé a Gand chez Seruais Manilius, au Pigeon / blanc,* M. DC / XLIII. *Et l'addition*: M. DC. XLV. *Sixième Discours. / Sur les Fieures Tierce, & Quarte, &c.* Chapitre II, 'De la Fieure Tierce', p. 97:

S'il ayme mieulx les poudres seules, le poids d'vne dragme plus ou moins des susdictes species Diacarthami est icy convenable, comme encore davantage autant de poudre qu'on appelle icy *Puluis indicus.*

(17) Sturm, Roland, *Febrifugi Peruviani Vindicarum &c.* (Delphis, 1659), Sectio Prima, p. 8:

Plerique autem in hoc nostro Belgio Pulverem Indicum vocant, só quod ex Indiis adferatur: Sed generale admodum est hoc nomen, cum plures adferantur ex Indiis; nec distinguit an Orientalis an Occiduus sit.

(18) Sturm, Roland, op. cit. p. 146:

Febr: Cort: Peru:
Modo di adoprare la
Corteccia chiamata
della Febre.

Qvesta Corteccia si porta dal Regno di Peru, e si chiama China, overo China della febre, laquale si adopra per la febre quartana, e terzana, che venga con freddo: s'adopra in questo modo, cioé:

Se ne piglia dramme due, e si pista fina, con passarla per setaccio; e tre hore prima incirca, che debba venir la febre si mette in infusione in un bicchiero di vino bianco gagliardissimo, e quando il freddo commincia á venire, ó si sente qualche minimo principio, si prende tutta la presa preparata, e si mette il patiente in letto.

Avertasi, si potrá dare detta Corteccia nel modo sudetto nella febre terzana, quando quella sia fermata in stado di molti giorni.

L' esperienze continua, há liberato quasi tutti quelli, che l' hanno presa, purgato prima bene il corpo, e per quatro giorni doppo non pigliar niuna sorte di medicamente, ma auvertasi di non darla se non con licenza delli Sig: Medici, acció giudicano si sia in tempo á proposito di pigliarla.

(19) Conygio, Antimo, *Pervviani Pvlveris Febrifvgi Defensor Repvlsvs a Melippo Protimo Belga* (1665), p. 4:

...La réputation de la poudre du Peru est tellement morte en cette ville, qu'on n'en parle plus, & que nous n'en ordonnons plus... (IX. Iul. M. DC. LV).

(20) Ramazzini, Bernardino, *Orationes Jatrici Argumenti &c.* Patavii. M. DCC. VIII.: *Oratio Tertia: Veram Febrium Theoriam & Praxim inter ea, quae af huc desiderantur esse recensendam. Habita die* 6. *Novembris* M. DCC. II, p. 102:

Profecto postquam hujus remedii usus innotuit, & praemissis justis purgationibus, non semel tantum, ut olim, sed plures ad dies exhiberi caeptus, donec febrile miasma fuerit penitús exantlatum, talem circa Febrium doctrinam, ac illam curandi methodum factam fuisse [mutationem] fateri oportet, qualem in re militari post inventum pulverem pyrium omnes norunt.

(21) Blanco-Juste, Dr Francisco Javier, *Historia del Descubrimiento de la Quina* (Madrid, 1934):

Recibi a su tiempo, hace ocho dias, dice, tu carta dada el dia 24 de Septiembre de 1764, y por ella fuí conmovido y regocijado en gran manera, pues contenia un bellisimo dibujo de la corteza de quina, juntamente con hojas y flores, cuyas flores nunca vistas por mi antes de ahora, me dieron verdadera idea de un género rarisimo, y muy diversa de la que adquiri por las figuras de Mr. Condamine. Estoy agradecidísimo por todo....

XI. Acknowledgements

This study on the History of Cinchona would have been much more arduous without the facilities granted by many Institutions, or the encouragement and assistance of individuals who have shown an interest in my researches.

Among the Institutions which I wish to acknowledge for placing at my disposal rare and valuable books and documents, I would like to single out especially the Linnean Society of London; the Department of Botany, British Museum (Natural History); the Herbarium, Royal Botanic Gardens (Kew); the Royal Geographical Society; the Wellcome Historical Medical Museum; the Library, Royal Society of Medicine; the British Museum (London); the Bodleian Library (Oxford); the Bibliothèque Nationale and the Musée de l'Homme (Paris).

Among the individuals, apart from all those anonymous officials who daily went to great trouble unearthing for me from their shelves, old and almost forgotten books, I must particularly mention Dr J. Ramsbottom and Mr A. H. G. Alston, Keeper and Principal Scientific Officer of the Botanical Department, British Museum (Natural History); Mr A. C. Townsend, Librarian of the General Library of the British Museum (Natural History), and Mr S. Savage, Assistant Secretary of the Linnean Society.

From abroad I have to acknowledge the kind co-operation of the Colombian Ambassador to the Holy See, Dr Carlos Arango-Vélez; that of Don Cristobal Bermúdez-Plata, Director of the Archivo General de Indias, Seville; that of Señorita Matilde López-Serrano, Director of the Biblioteca de Palacio, Madrid, and that of Dr E. Harthterré in Lima, Don Guillermo Lohmann-Villena, Secretary at the Peruvian Embassy in Madrid, and Don Manuel Ballesteros Gaibrois in Valencia, who kindly helped me to get some literature and documents from the Vatican Library, the Spanish Libraries and the Peruvian Libraries.

Last, but not least, I would like to name three people without whose contribution the accomplishment of this work would have been hardly possible: Mlle. Marie-José Nemry most assiduously accompanied me in all my researches, handling all my notes for me and collaborating with me in putting my text into English. Dr Robert M. Evans of Liverpool and Mr F. N. L. Poynter, Deputy Librarian, the Wellcome Historical Medical Museum, who kindly read and put the final touches to the English version of the work.

Explanation of Plates

Plate 10

Linnaeus, *Materia Medica* 1749. Annotations. (Courtesy of the Linnean Society.)

Plate 11

Beginning of Chapter 26 of Fray Antonio Vázquez de Espinosa's Manuscript *Compendio y Descripcion de las Indias Ocidentales*, in possession of the Vatican Library, Barberini Collection (No. 3584), the first known work to mention the *Quinaquina* Tree (Peruvian Balsam Tree) and to give a description of its qualities. Therein it is also stated that it is to be found in the neighbourhood of the City of La Plata (modern Sucre), former capital of Bolivia, in the Province of Charcas. (Courtesy of the Vatican Library.)

Plate 12

A map of South America, just before Fray Antonio Vázquez de Espinosa's description of the New World, 1595, clearly showing the location of the Province of Charcas. Haggis's sketch in his work (*Bulletin of the History of Medicine*, 1941), vol. x, p. 428, locating Chacas or Charcas in Ecuador is erroneous. This map has the singularity of depicting South America from the point of view of Europeans approaching the Continent from east to west, giving the impression that Peru is in the north of the Continent and Brazil in the south. (Personal collection.)

Plate 13

An enlarged copy of the section of the map (Plate 12) giving details of the Province of Charcas, and showing the geographical relations between La Plata, Potosí and La Paz (the present capital of Bolivia), all three cities closely connected with the history of Cinchona. (Personal collection.)

Plate 14

Page of the Quichua Dictionary of 1614 (wrongly attributed to Francisco del Canto, the Printer), to which La Condamine refers. Here first, the word alluded to by La Condamine appears as 'Quinaaylliclla', not 'Quina-ai', with the meaning 'Mantellina de india' instead of 'Mantelilla india'. And secondly, Haggis's double word for Quinua is written 'Quinuaiquinua', instead of 'Quinua, quinua', with the meaning 'a certain leguminous plant thus called' (cierta legumbre llamada assi). (Courtesy of the British Museum.)

Plate 15

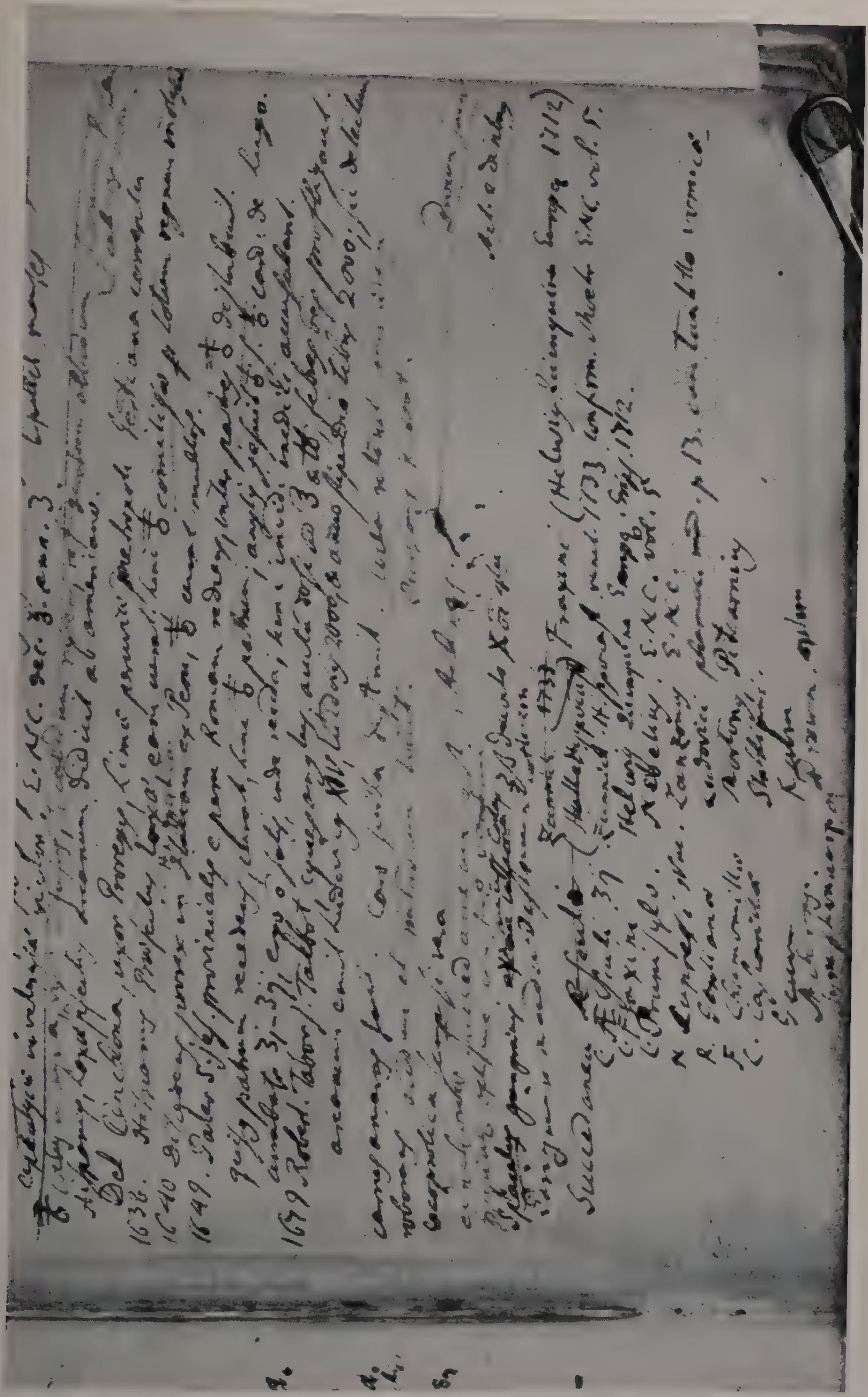
Page of the 1604 edition of the *Vocabulario en la Lengua General del Peru* of Fray Juan Martínez, where La Condamine's word appears this time written as 'Quinray lliclla', and Haggis's double word for Quinua as 'Quinua, quinua', here also with the meaning 'a certain leguminous plant thus called' (cierta legumbre llamada assi). (Courtesy of the British Museum.)

Plate 16

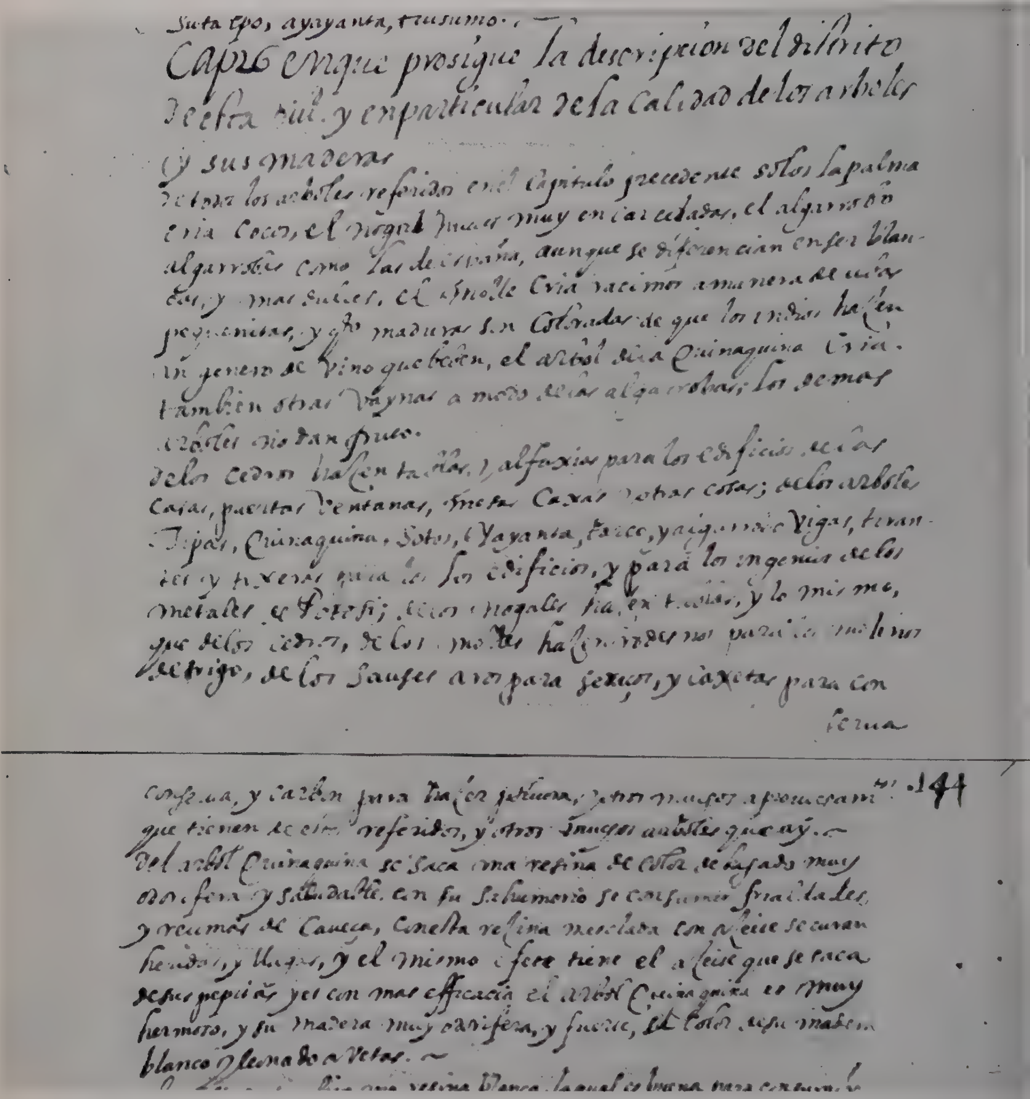
Page of Fray Martinez' *Vocabulario* giving the words 'Queñua' and 'Queñuaqueñua', with the meaning, 'tree thus called' (arbol llamado assi) for the former, and 'grove of this' (arboleda desto) for the latter. The same words occur in the 1586, 1603 and 1614 editions. (Courtesy of the British Museum.)

Plate 17

Fig. 1. Print of the Cinchona Tree in the *Historiarum Anatomicarum, & Medicarum Rariorum, Centuria V & VI*, by Thomas Bartholinus, published in 1661; the first Treatise in Europe to give an illustration of the Cinchona Tree. Bartholinus states that he received this drawing from Hieronymus Badus through their common friend Heinrich von Moinichen. (Courtesy of the Royal Society of Medicine.)



Linnaeus, *Materia Medica*, 1749—Annotations



Suta tpo, ayrayanta, tiusumo. —

Capº 6 en que prosigue la descripcion del distrito de esta ciud. y en particular de la calidad de los arboles y sus maderas

De todos los arboles referidos en el capitulo precedente solos la palma cria cocos, el nogal nueces muy encarceladas, el algarrobo algarrobas como las de españa, aunque se diferencian en ser blancas, y mas dulces, el molle cria racimos a manera de uvas pequeñitas, y quando maduras son coloradas de que los indios hazen un genero de vino que beben, el arbol de la quinaquina cria tambien otras vaynas a modo de las algarrobas; los demas arboles no dan fruto.

De los cedros hazen tablas, y alfaxias para los edificios, de las cajas, puertas ventanas, mesas caxas y otras cosas; de los arboles tipas, quinaquina, sotos, yayanta, tarco, y algunos hazen vigas, tirantes y tixeras para los edificios, y para los ingenios de los metales de Potosi; de los nogales tablazon, y lo mismo que de los cedros, de los molles hazen ruedas para los molinos de trigo, de los sauces arcos para zedazos, y caxetas para conserua, y carbon para hazer polvora, y otros muchos aprovechamientos que tienen de ellos referidos, y otros muchos arboles que ay. —

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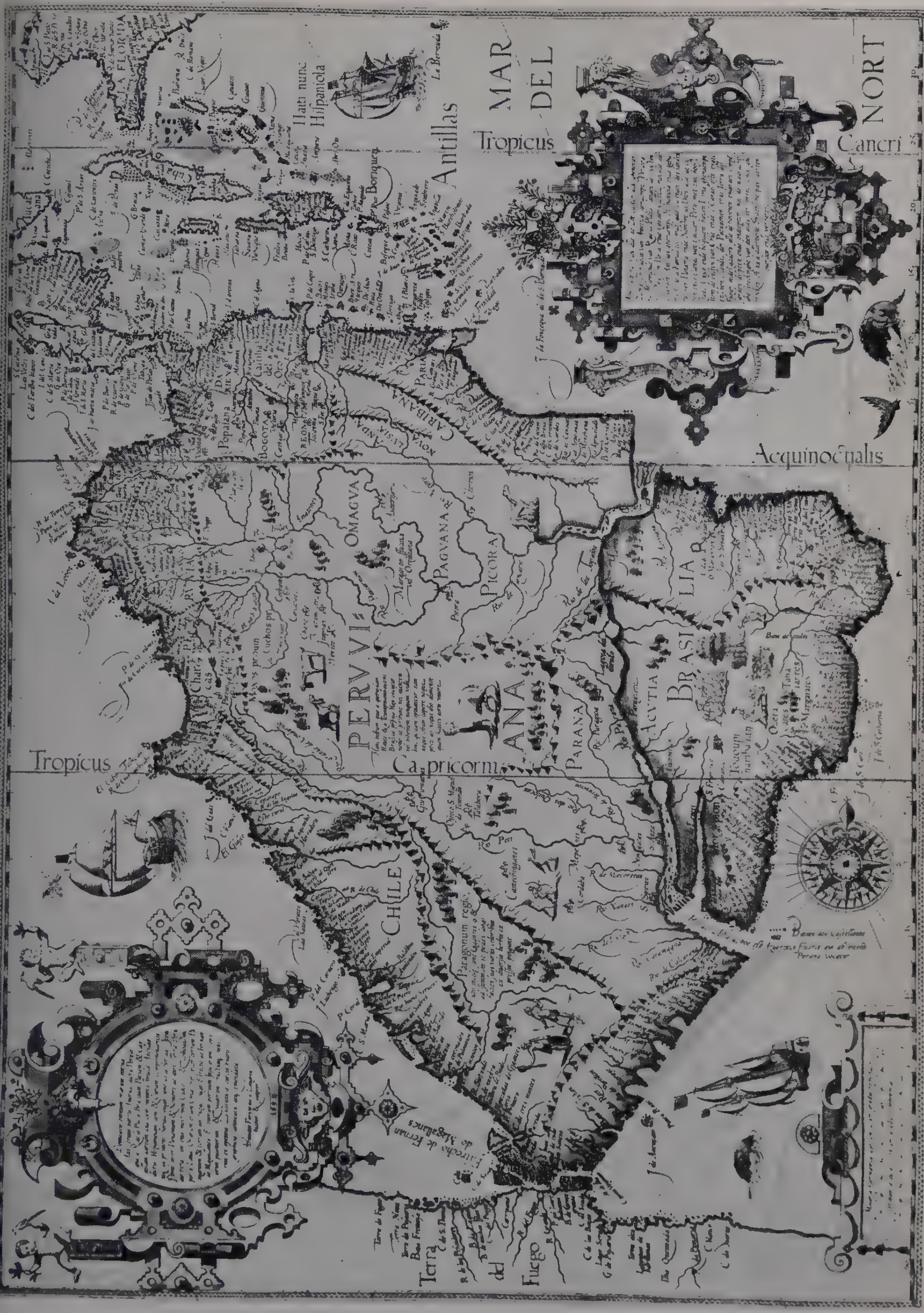
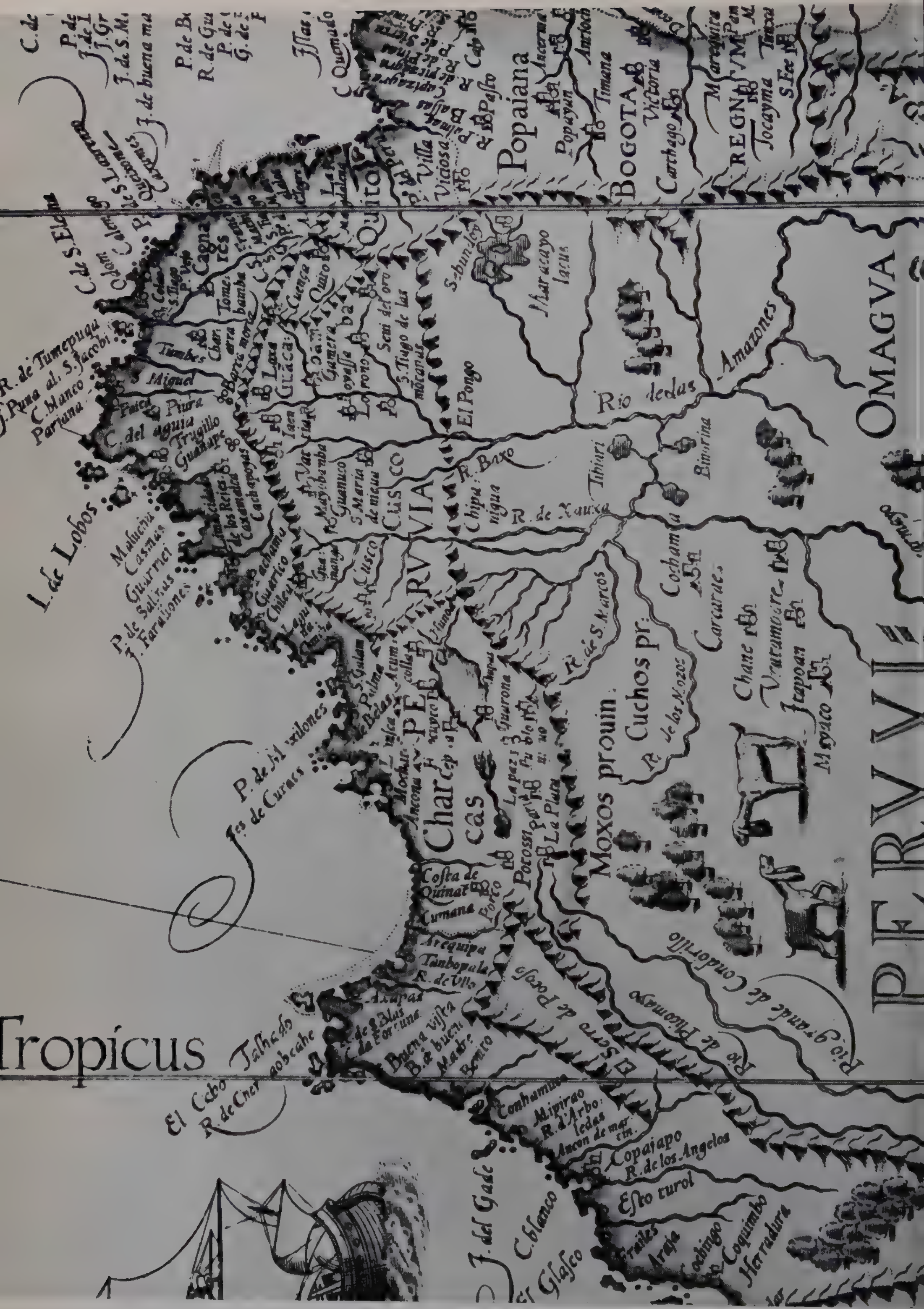
Del arbol quinaquina se saca una resina de color dorado muy odorifera y saludable. con su sahumerio se consumen frialdades, y reumas de cabeza, con esta resina mezclada con azeite se curan heridas, y llagas, y el mismo efecto tiene el azeite que se saca de sus pepitas y es con mas efficacia el arbol quinaquina es muy hermoso, y su madera muy odorifera, y fuerte, el color de su madera blanco y leonado a vetas. ~

una resina blanca la qual es buena para

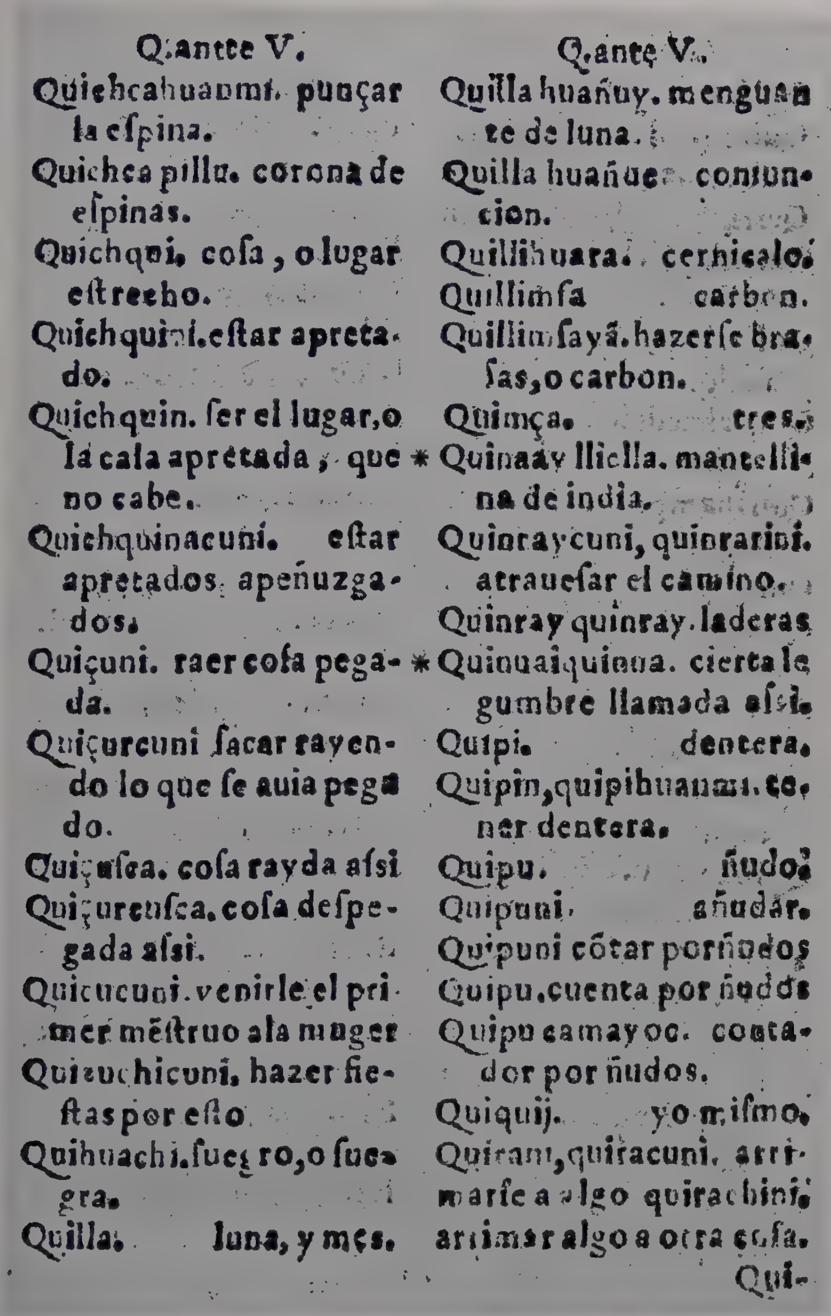
First mention of the Peruvian Balsam Tree



Map showing the Province of Charcas, *circa* 1595



Enlarged portion of Plate 12



Q. ante V.

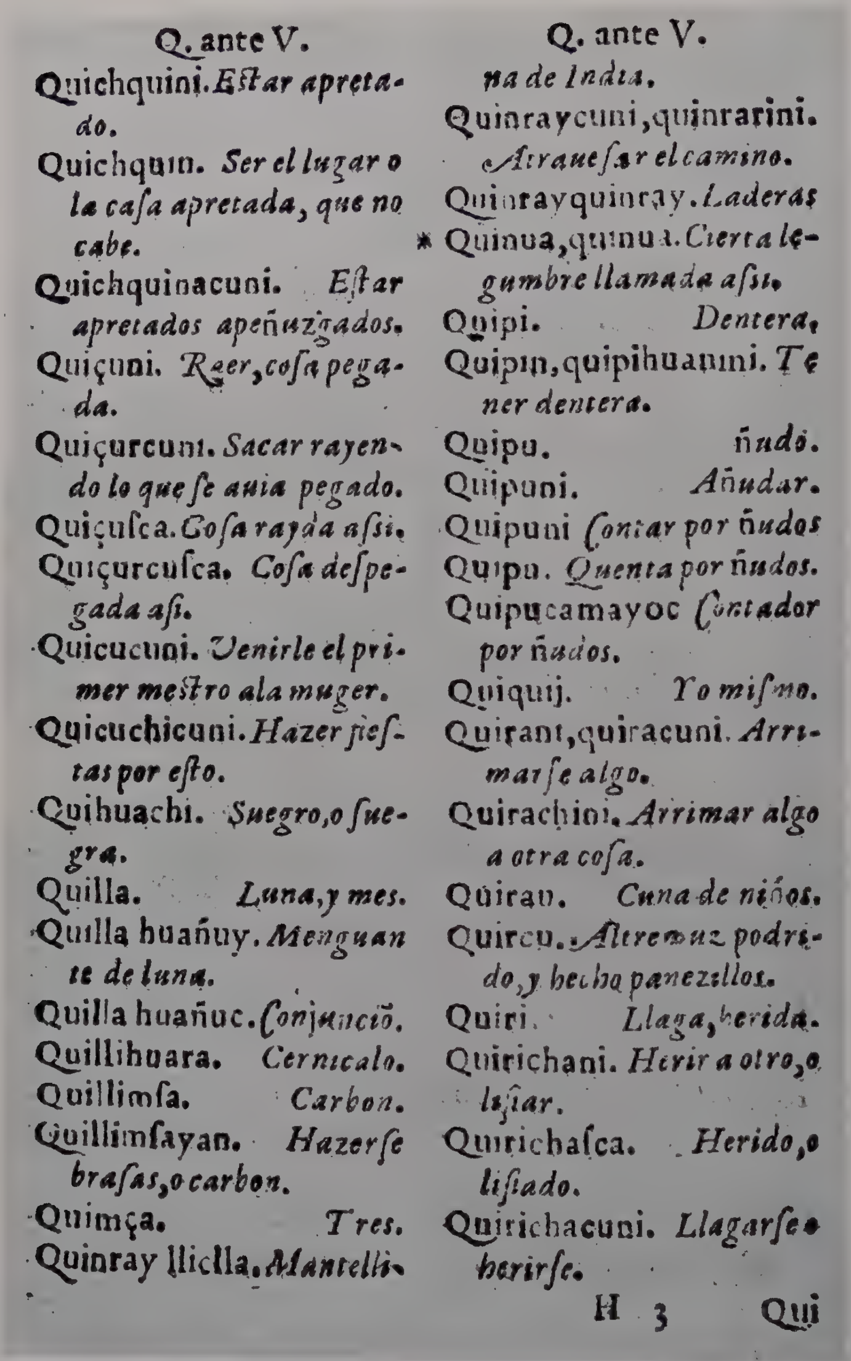
Quichcahuanmi. punçar la eſpina.
Quichca pillu. corona de eſpinas.
Quichqui. coſa, o lugar eſtrecho.
Quichquini. eſtar apretado.
Quichquin. ſer el lugar, o la caſa apretada, que no cabe.
Quichquinacuni. eſtar apretados apeñuzgados.
Quiçuni. raer coſa pegada.
Quiçurcuni ſacar rayendo lo que ſe auia pegado.
Quiçuſca. coſa rayda aſsi
Quiçurcuſca. coſa deſpegada aſsi.
Quicucuni. venirle el primer mẽſtruo ala muger
Quicuchicuni. hazer fieſtas por eſto
Quihuachi. ſuegro, o ſuegra.
Quilla. luna, y mes.

Q. ante V.

Quilla huañuy. menguante de luna.
Quilla huañuc. coniuncion.
Quillihuara. cernicalo.
Quillimſa carbon.
Quillimſayã. hazerſe braſas, o carbon.
Quimça. tres.
* Quinaay lliclla. mantellina de india.
Quinraycuni, quinrarini. atraueſar el camino.
Quinray quinray. laderas
* Quinuaiquinua. cierta legumbre llamada aſsi.
Quipi. dentera.
Quipin, quipihuanmi. tener dentera.
Quipu. ñudo.
Quipuni. añudar.
Quipuni cõtar por ñudos
Quipu. cuenta por ñudos
Quipu camayoc. contador por ñudos.
Quiquij. yo miſmo.
Quirani, quiracuni. arrimarſe a algo quirachini. arrimar algo a otra coſa.

Qui-

Page of the Quichua Dictionary of 1614



Q. ante V.

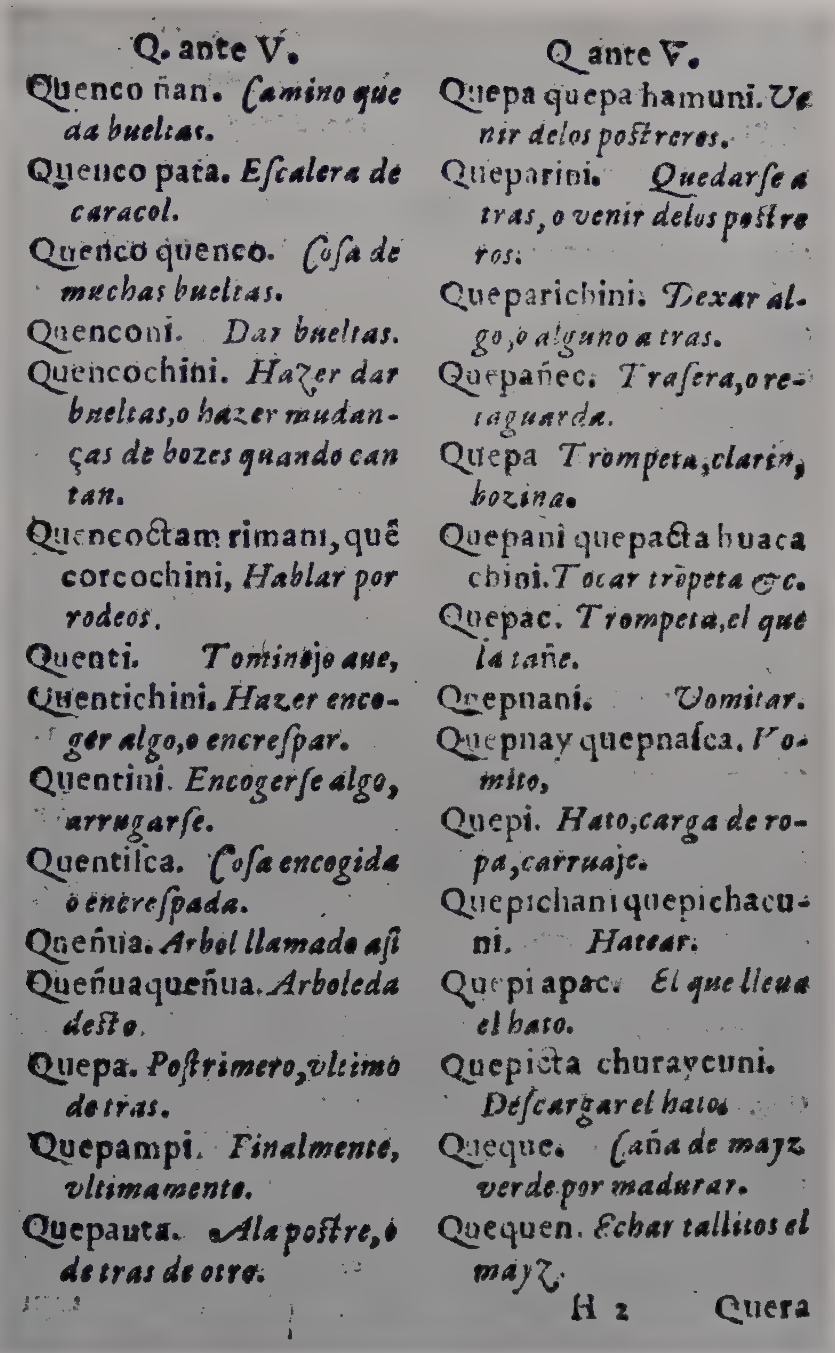
Quichquini.	*Eſtar apretado.*
Quichquin.	*Ser el lugar o la caſa apretada, que no cabe.*
Quichquinacuni.	*Eſtar apretados apeñuzgados.*
Quiçuni.	*Raer, coſa pegada.*
Quiçurcuni.	*Sacar rayendo lo que ſe auia pegado.*
Quiçuſca.	*Coſa rayda aſsi.*
Quiçurcuſca.	*Coſa deſpegada aſsi.*
Quicucuni.	*Venirle el primer meſtro ala muger.*
Quicuchicuni.	*Hazer fieſtas por eſto.*
Quihuachi.	*Suegro, o ſuegra.*
Quilla.	*Luna, y mes.*
Quilla huañuy.	*Menguante de luna.*
Quilla huañuc.	*Conjunciõ.*
Quillihuara.	*Cernicalo.*
Quillimſa.	*Carbon.*
Quillimſayan.	*Hazerſe braſas, o carbon.*
Quimça.	*Tres.*
Quinray llicla.	*Mantellina de India.*

Q. ante V.

Quinraycuni, quinrarini.	*Atraueſar el camino.*
Quinrayquinray.	*Laderas*
* Quinua, quinua.	*Cierta legumbre llamada aſsi.*
Quipi.	*Dentera.*
Quipin, quipihuanini.	*Tener dentera.*
Quipu.	*ñudo.*
Quipuni.	*Añudar.*
Quipuni	*Contar por ñudos*
Quipu.	*Quenta por ñudos.*
Quipucamayoc	*Contador por ñudos.*
Quiquij.	*Yo miſmo.*
Quirani, quiracuni.	*Arrimarſe algo.*
Quirachini.	*Arrimar algo a otra coſa.*
Quirau.	*Cuna de niños.*
Quircu.	*Altremuz podrido, y hecho panezillos.*
Quiri.	*Llaga, herida.*
Quirichani.	*Herir a otro, o liſiar.*
Quirichaſca.	*Herido, o liſiado.*
Quirichacuni.	*Llagarſe o herirſe.*

H 3 Qui

Page of the 1604 edition of the *Vocabulario en la Lengua General del Peru*



Q. ante V.

Quenco ñan. *Camino que da bueltas.*

Quenco pata. *Eſcalera de caracol.*

Quenco quenco. *Coſa de muchas bueltas.*

Quenconi. *Dar bueltas.*

Quencochini. *Hazer dar bueltas, o hazer mudanças de bozes quando cantan.*

Quencoctam rimani, quẽcorcochini, *Hablar por rodeos.*

Quenti. *Tominejo aue,*

Quentichini. *Hazer encoger algo, o encreſpar.*

Quentini. *Encogerſe algo, arrugarſe.*

Quentiſca. *Coſa encogida o encreſpada.*

Queñua. *Arbol llamado aſi*

Queñuaqueñua. *Arboleda deſto.*

Quepa. *Poſtrimero, vltimo de tras.*

Quepampi. *Finalmente, vltimamente.*

Quepanta. *Ala poſtre, o de tras de otro.*

Q ante V.

Quepa quepa hamuni. *Venir delos poſtreros.*

Queparini. *Quedarſe a tras, o venir delus poſtreros.*

Queparichini. *Dexar algo, o alguno a tras.*

Quepañec. *Traſera, o retaguarda.*

Quepa *Trompeta, clarin, bozina.*

Quepani quepacta huacachini. *Tocar trõpeta &c.*

Quepac. *Trompeta, el que la tañe.*

Quepnani. *Vomitar.*

Quepnay quepnaſca. *Vomito,*

Quepi. *Hato, carga de ropa, carruaje.*

Quepichani quepichacuni. *Hatear.*

Quepi apac. *El que lleua el hato.*

Quepicta churaycuni. *Deſcargar el hato.*

Queque. *Caña de mayz verde por madurar.*

Quequen. *Echar tallitos el mayz.*

H 2 Quera

Page of the *Vocabulario*...1604

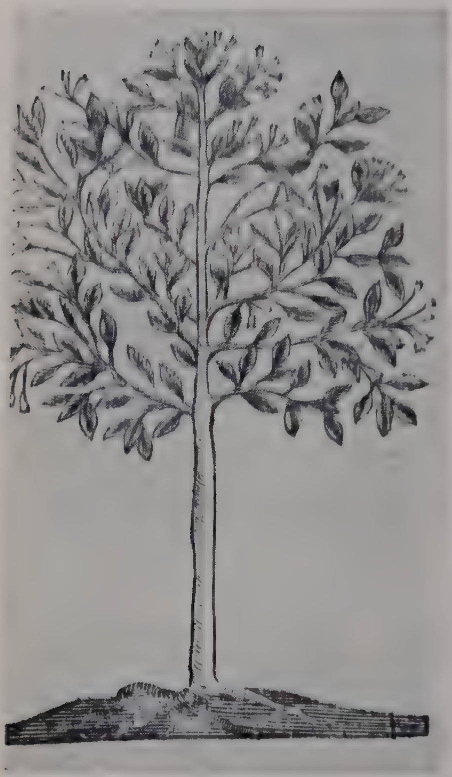


Fig. 1. The earliest printed illustration of the Cinchona Tree (1661)

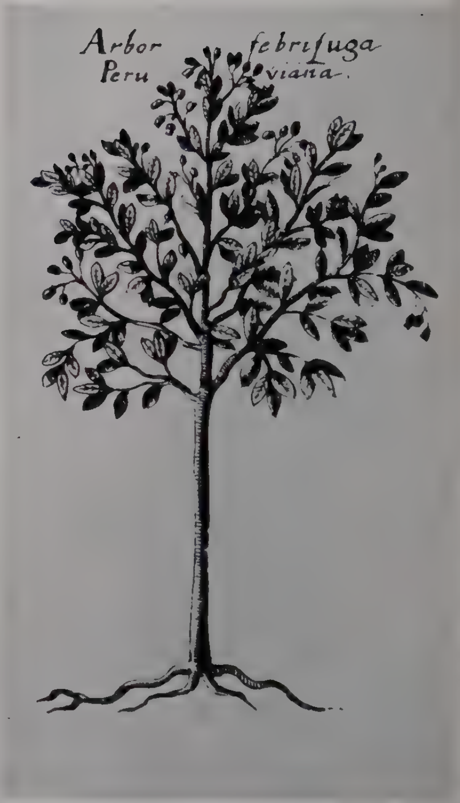
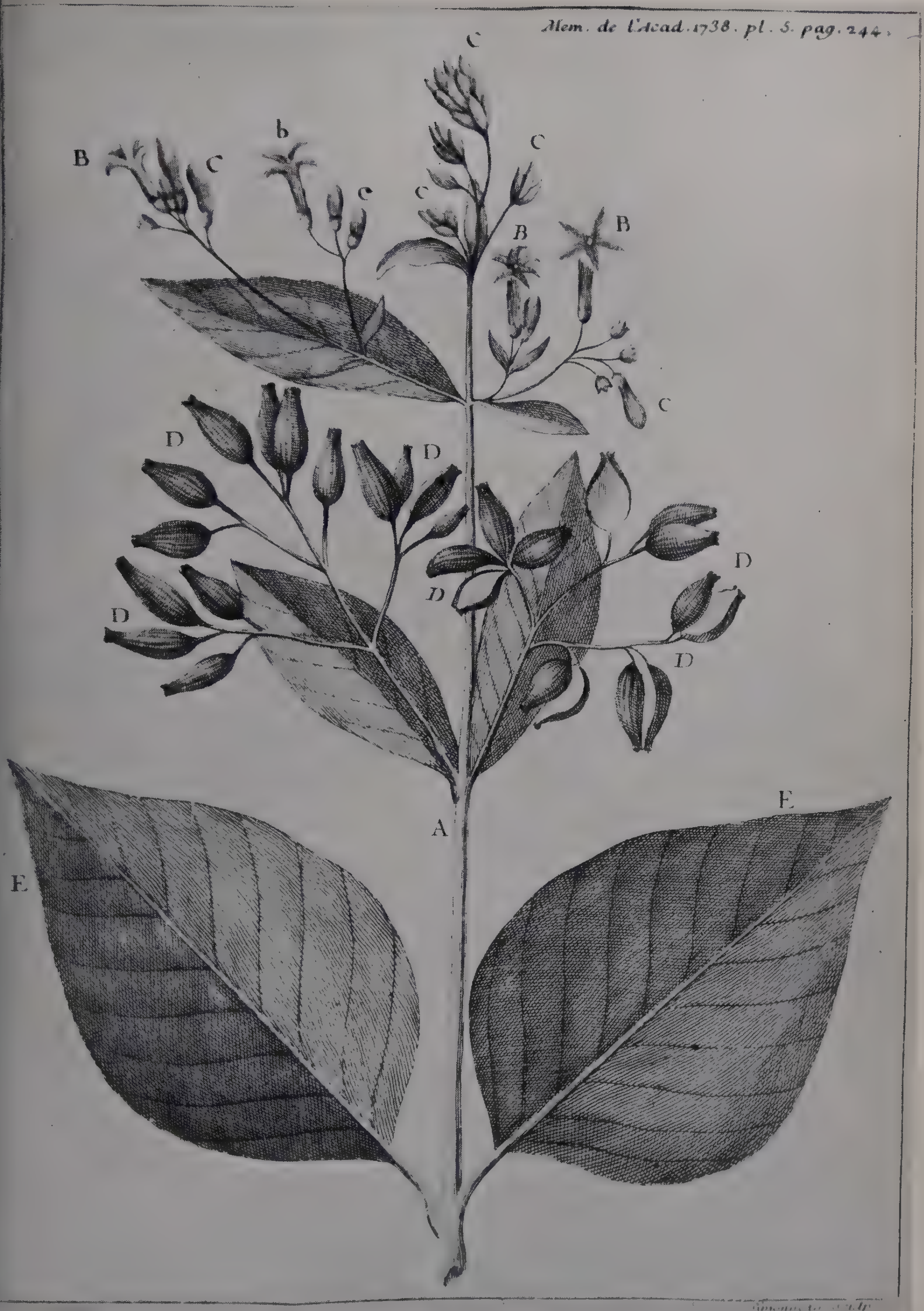


Fig. 2. The Cinchona Tree in Jonston's *Dendrographias* (1662)


Mem. de l'Acad. 1738. pl. 5. pag. 244.
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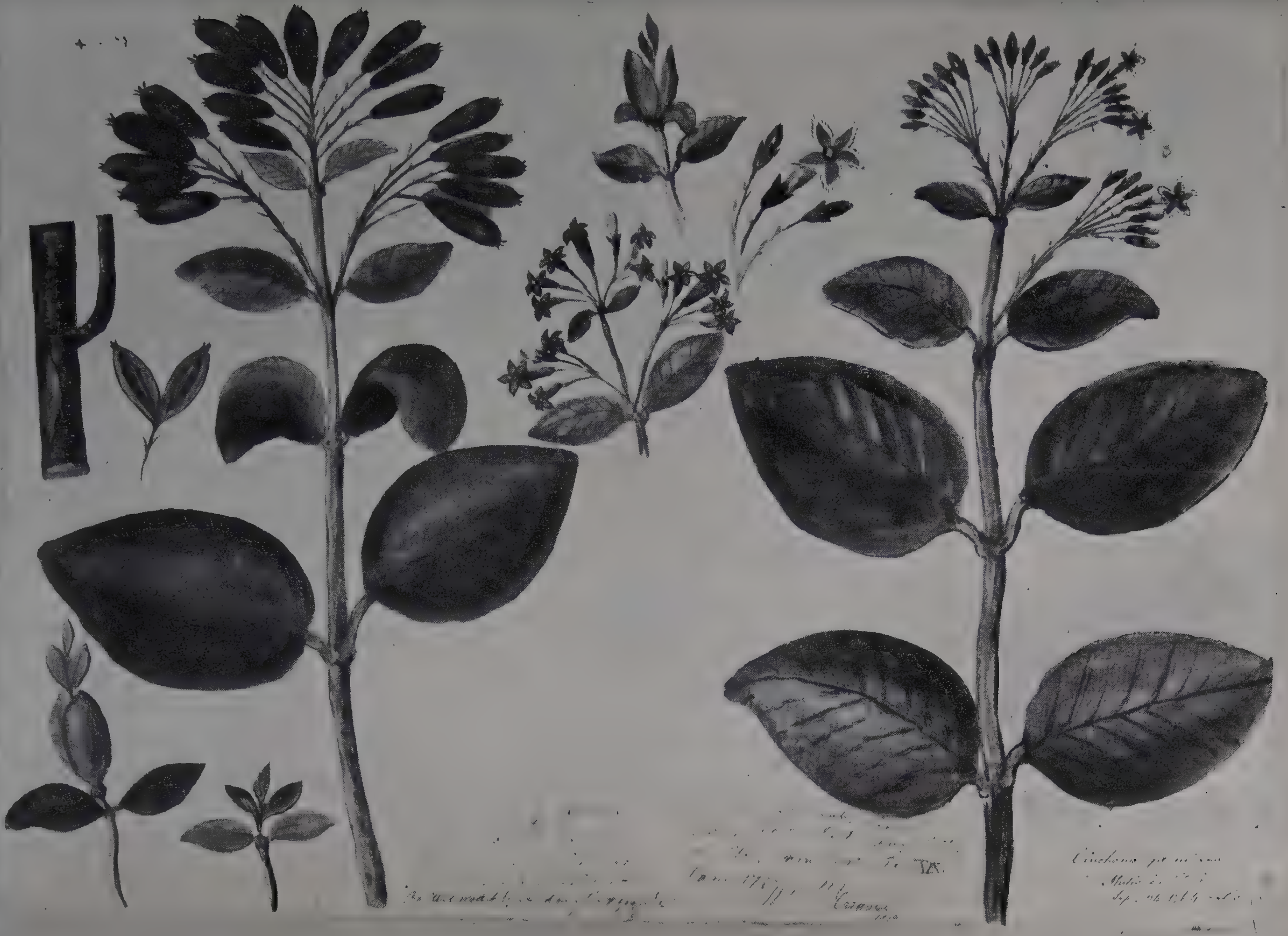
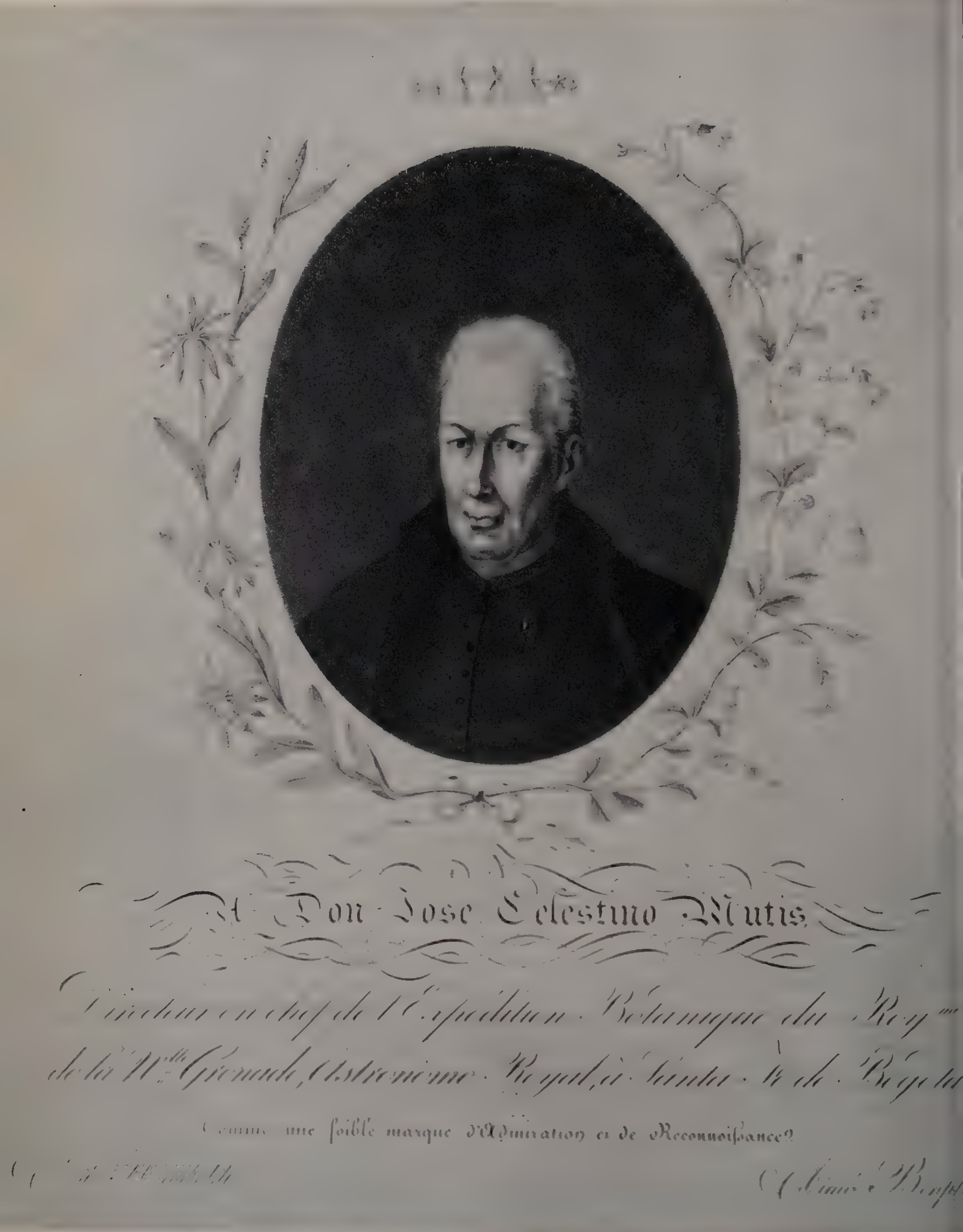
La Condamine's drawing of the Cinchona Tree

General view of Loja


Cinchona
IX



A Don Jose Celestino Mutis

Directeur en chef de l'Expédition Botanique du Roy^{me} de la N^{lle} Grenade, Astronome Royal, à Santa Fé de Bogota

Comme une foible marque d'Admiration et de Reconnoissance

Aimé Bonpl

Fig. 2. View of the Cinchona Tree, published in John Jonston's *Dendrographias: sive Historiae naturalis et fructibus...libri X*, in 1662; the second illustration of the Cinchona Tree to be published in Europe. (Courtesy of the Wellcome Historical Medical Museum.)

Plate 18

Reproduction of La Condamine's drawing of the Cinchona Tree which appeared with his communication in the Memoir of the Academy of Sciences of Paris, in July 1738. (Courtesy of the Linnean Society.)

Plate 19

General view of Loja, town of which López de Cañizares was Corregidor and from which it is said that he sent the bark to Lima for the cure of the Countess de Chinchón. In the background can be seen the *Cordillera de Cajanuma*, where La Condamine made his drawing of the 'Fruit, flowers and leaves' of the Cinchona Tree. (Courtesy of Dr José E. Muñoz and Virgilio Poredes-Borja, Quito, Ecuador.)

Plate 20

Santisteban's coloured drawing of the Cinchona Tree, which he gave to Mutis, and which Mutis sent to Linnaeus in 1764. (Courtesy of the Linnean Society.)

Plate 21

Engraved portrait of Mutis, published in Humboldt and Bonpland's work, *Plantae Aequinoctiales* (1808), as a tribute to the learned Spanish botanist, framed with the branches of the plant which Gronovius named in honour of Linnaeus (*Linnaea borealis*, right), and that which Linnaeus fil. named in honour of Mutis (*Mutisia*, left). (Courtesy of the Linnean Society.)

(Owing to the loss in the post of one of the proofs of this paper, the following emendations were not made in the final text)

ADDENDUM

to 'A Critical Review of the Basic Facts in the History of Cinchona',

by Dr Jaime Jaramillo-Arango

[*Journ. Linn. Soc. Lond., Bot.* Vol. LIII. Additional leaf to be inserted at the end of No. 352]

p. 279, line 4: *for* which represented *read* which then represented

p. 283, line 6: *for sentence* So far, ...a reply yet, *substitute* According to the Keepers of the Jesuit Archives in Rome (Fr. José Teschitel) and Lima (Fr. José Torrijos) to whom we have written asking for particulars concerning this document and for a copy of it, it is not to be found in either place. Fr. Vargas-Ugarte informed the latter that he took the reference from Enrique Torres-Saldamando's work *Los Antiguos Jesuitas del Perú*, (1882). Once more, Torres-Saldamando fails also to give the complete text of the letter. He states, however (pp. 190–191), that it is to be found in the Archivo Nacional de Lima (Legajo No. 1179). Notwithstanding this reference, we have been unable to obtain a copy of this document: Dr. E. Harth-terré, our correspondent in Lima, informs us that some time ago one of the sections of the Archivo Nacional was incorporated into the Biblioteca Nacional, and that unfortunately, as it is known, in the year 1942 the Library suffered severe losses in a disastrous fire. As a consequence, he has been unable to confirm the existence of the document.

p. 283, line 12: *for* author *read* Canezza

p. 288, line 13 from bottom: *for* Myroxylon peruiferum v. [vulgo] *Quinoquino*: *read* *Myroxylon peruiferum* v. [vernaculo] Quinoquino:

p. 288, last line: *for* taking ounces *read* taking four ounces

p. 289, line 27: *for* quina *read* quiuna

p. 289, ftnote 1: *for* Cabelleros *read* Caballeros; for *Revista Javerina* read *Revista Javeriana.*

p. 290, line 13: *for* and the bark *read* and for the bark

p. 291, ftnote 1: *for* [80 sq.cm.] *read* [84·7 cm.]

p. 292, ftnote 1 (*d*): for *neuvamente* read *nuevamente*

p. 295, line 19 from bottom: *for* Soer's *read* Soers's

p. 296, line 18: for *Pulius* read *Puluis*

p. 296, line 24: *after* see *read* (Section VIII),

p. 296, ftnote 5: *for* Michael Belga [Bolag] *read* Miguel Belga [Michel Bolag],

p. 300, ftnote 4: *for* Plate I *read* Plate 10.

p. 301, ftnote 4: for *Ayla* read *Ayala*

p. 302, line 16 from bottom: *for* López Ruiz *read* López-Ruiz

p. 303, line 5 from bottom: *for* Corteccis *read* Corteccia

p. 304, line 21: *for* asinismo *read* asimismo

p. 304, line 17 from bottom: *for* lipmiarla *read* limpiarla

p. 304, line 7 from bottom: *for* maciessen *read* naciessen

p. 305, line 5: *for* [vulgo] *read* [vernaculo]

p. 305, line 12: *for* tembien *read* tambien

p. 305, line 21: *for* llagas, *read* llagas.

p. 306, line 8: *for* e Ingenios *read* é Ingenios

p. 306, line 7 from bottom: *for* overa *read* o vero

p. 309, line 11: *for* Virgilio Poredes-Borja *read* Dr Virgilio Paredes-Borja

The ontogeny of the stem of the Common Bryony, Tamus communis Linn.

By I. H. Burkill

(With 52 Text-figures)

[Read 13 December 1947]

I. Introduction

In 1878 Solms-Laubach described (*Bot. Zeitung*, **36**, 81) the way in which the cotyledon of *Tamus communis* usurps the cauline end of the forming embryo, pushing the morphological apex to one side where it is caused to lie in a shallow pit. The rim of this pit is the amplexicaul base of the cotyledon (see Velenovsky, *Vergleich. Morphologie d. Pflanzen* (1905), 321). The rim rises on the side opposite to the cotyledon into curious ears (see Fig. 1)—ears that certain botanists have claimed to be a second cotyledon. Development proves that they are not; moreover, they are never vasculated, which is against the theory of these botanists, though not complete disproof. From the stage at which Solms-Laubach left his investigations, I begin mine.

By 'stem' in my title I mean an axis that has extended; for instance, there is a cauline apex in the embryo, but no stem as extension has not commenced. The cauline apex grows to an organized bud with foliar emergences which enlarge into foliar organs; and not until after that the stem appears and spaces out the foliar organs. I am occupied with the controls under which it appears and develops, recognizing that evolution works through the controls. If they be intensified or relaxed, the end-product is changed. This study is in origin an attempt to improve the accepted classification of the family Dioscoreaceae by seeking out the phylogeny behind the taxonomy in which I am examining as many species of the family as I can keep alive. The study of *Tamus* has advanced beyond that of the others because it has been abundantly available. The others perhaps offer fewer complexities. I shall end this paper with observations bearing on my belief that the genus *Tamus* originated in Africa.

It is necessary that I describe the tuber because the tuber is a cauline structure. It and the aerial stems are very divergently differentiated. *Tamus*, as a geophyte annually makes and discards its aerial stems, but the tuber, though it be equally cauline, is perennial. How widely these two parts of the plant contrast is obvious. No more of the first is preserved at the end of the annual cycle than just enough for a fresh start: the rest is thrown away by an act of self-pruning. The part kept is a stemless bud or buds attended by the tuber. These buds make preparation for branching by initiating in turn buds that are lateral to them, all the lowest of which have in equal degree the potentiality of becoming annual stems. Incidentally, I shall call attention to the great care taken of them and to the impressive multiplication of apices in them, and to the heavy toll taken of them in England by winter frosts, and to the manner in which the plant, as it grows in England, makes use of all the months of the year for some measure of activity. It does not reach the Scottish border. Its winter growth is slow.

Tamus may be regarded as a genus evolved from *Dioscorea* by a change in the time of the death of the ovary walls. In *Dioscorea*, as the seeds ripen, the walls die and dry, and a capsule results: in *Tamus* they live beyond this time, serving as water-stores and never dry, so that a functional capsule becomes impossible, and the means of dispersal are turned over from the wind to the birds. The other characters of mark in Dioscoreas are undisturbed: *Tamus* remains a climber and a tropophyte. The height to which it climbs (say 3 m.) suggests evolution in a land of scrub. Of its two species, *T. communis*, if it were without apical dominance, would be abundantly ramose; but apical dominance is powerfully developed; and it is not ramose. The other species, *T. edulis* Lowe, seems to be similar. It is clear that *T. communis* attains a greater height above the soil by remaining unbranched than it would if branched (see p. 372) and it is plausible that the superposing of apical dominance on a stem with a great abundance of buds indicates that the genus has evolved towards life in deeper scrub, meeting in this way the necessity of elongation. As will be shown on p. 377, it shares with certain South African Dioscoreas, which grow as freely branched plants in rocky heath, a series of characters that collectively indicate a great measure of affinity, and it is recorded that *T. communis* itself invades the Dalmatian rocky heath (Beck v. Managetta, in Engl. u. Drude, *Die Vegetat. d. Erde* (1901), 4, 153, 158 and 398). At present no closer affinity is evident than with these plants of Cape Colony. Further, as strengthening the belief that its origin was in Africa, there are resemblances between it and certain Madagascan Dioscoreas. Its route from Africa into the Mediterranean would be on the Atlantic side, over against which it left *T. edulis* in the Canary Islands and Madeira.

On p. 329 I call attention to the deployment of the stems of *T. communis* when they are several from a tuber, as they reach the light; and on p. 365 to the specialization of a 'Spring Push' by which advantageous positions are snatched on competing vegetation; and I link, here, the rapidity of the spring push with the circumstance that the plant gains in its competition by not thickening its stem in the usual degree below the part at which it suspends its weight, but so grows as to increase in circumference upwards to it. I show (p. 361) that there is a progressing change of divergence from the base of the stem upwards and call attention to a time-limited differential power of growth between the foliar emergence and the axis that is potent in determining foliar divergence. That foliar organs, although dependent on the axis for their initial growth, outgrow dependence and complete themselves autochthonously, even to a degree that appears of disadvantage to the axis, is a view that has not had the emphasis which botanists should have given to it.

By statistical analyses of measurements of lengths of internodes I have found the stem curiously bifacial. Section 19 explains this.

I give my interpretations of the influences which, determining the leaf-divergence, make leaf-arrangement distichous at the base and tristichous over the rest of the stem.

2. From fruit ripening to the end of the seedling's first season

The seed of *Tamus* is not ready to germinate when the berry is ripe. Experiments have shown that the appropriate temperatures occur in spring and autumn; and that prior to their arrival six months under moist conditions must have passed—moist conditions such as are not provided by the English summer; and therefore germination is ordinarily in spring after the humidity of winter, though experiments are showing that the time of germination becomes less exact if the seed be dried out after being freed from the berry. As a consequence the attainment of readiness to germinate in the first spring after its ripening is made unlikely; and it is made still more unlikely by reason of delays which accompany its freeing from the berry; for birds do not eat the berries readily, and only quite late in the autumn inclement weather breaks them up. The seed-dispersal position consequently is that a bird very rarely transports a seed to a new place, and extremely rarely so early in the autumn as to lead to germination in the next spring. Seeds almost invariably germinate when fifteen to eighteen months old.

The seed on being freed is washed by rain into a crack or hollow of the soil, where, by a considerable shrinkage on drying and an expansion on becoming moist again, it works its way mechanically downwards. The depth that is reached is discussed in section 4 (p. 321). The six months of after-ripening are six months of sinking. A seed liberated in September or October may perhaps be ready to germinate in March or April, but a seed not liberated until December cannot be ready; it rests in the summer, and with a further sinking into the soil has in England a certainty of readiness to germinate as the second spring approaches.

When the seed is ripe the embryo occupies the outer part of a radius in it, the radicle touching the inner side of the seed-coats. The embryo has by this time become cigar-shaped, the thicker end inwards. Around the end of the radicle the seed-coats are now subjected to digestion; it would seem that this is by the excretion which the cotyledon uses on the endosperm, and that the excretion seeps down to the surface of the root-cap, but is prevented from passing between it and the seed-coats, as the digestion occurs in the form of a ring; and the ring when it gives way before the pressure of the growing embryo, permits the radicle to extrude. The seed-coats are leathery enough for the little area within the ring to hold together in the form of a lid on a hinge which is folded back before digestion is altogether complete. The radicle lifts the lid; and the part of the embryo deeper in the seed follows it through the hole until the cauline pit is outside, whereupon the thicker base of the cotyledon jams (see Fig. 1). Having jammed, it becomes firmly fixed by an increase of thickness on either side of the hole; and it remains as a plug while the cotyledon absorbs the food in the endosperm and passes it to the outside.

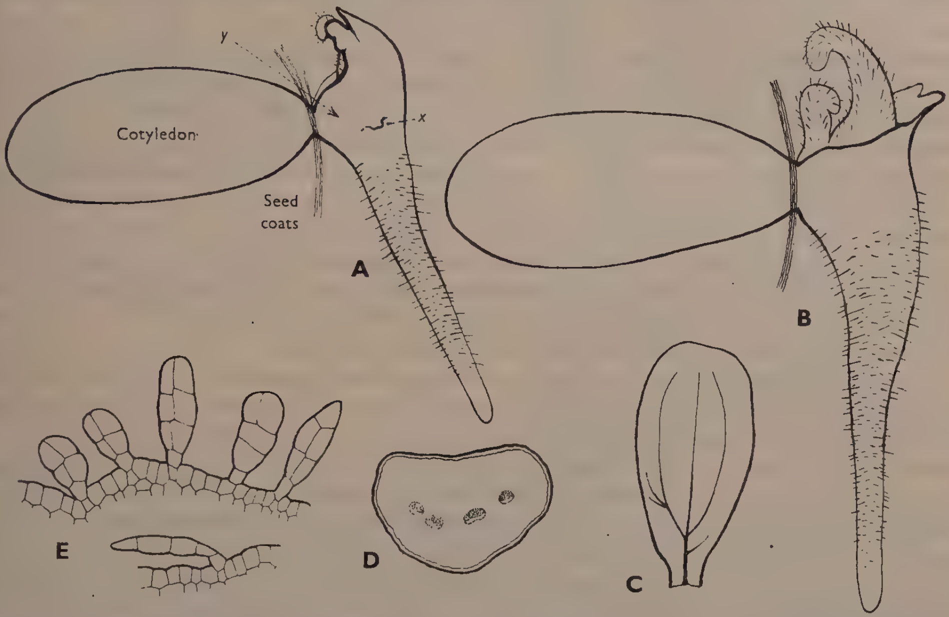


Fig. 1. **A.** The seedling newly germinated: x and y are explained in the text. **B.** The seedling ten days old. **C.** The first venation formed within the cotyledon seen from above. **D.** The cotyledon in vertical section, showing the plane in which the bundles lie. **E.** Colleters such as appear on the leaves in **B**, × 40. Most colleters are clavate as in the upper of the two drawings, but some are shortly filamentous as in the lower.

A rare mishap is for the hole in the seed-coats to be too small—so small that the embryo jams prematurely with the cauline pit inside. Death of the seedling is thereon inevitable.

The cotyledon, initially dorsiventral, but not pronouncedly so, ultimately is globose, for it fills the cavity of the seed on consuming the endosperm. The dorsiventral layout of its first vascular bundles is indicated in Fig. 1; slender additional bundles, appearing between these, turn the system into a hollow net.

It must be accepted that the rim of the cauline pit delimits the hypocotyl towards the epicotyl on the ground that it is the base of the cotyledon. Above the rim there is nothing and later little that can be claimed to be epicotyl. Therefore Dutrochet (*Nouv. Ann. du Mus. Hist. Nat.* (1835), 4, 169), Bucherer (*Bibliotheca bot.* (1889), Heft 16, p. 4), Gardiner & Hill (*Proc. Camb. Phil. Soc.* (1902), **11**, 445), and others unwarrantably state that the tuber is formed in the epicotyl. Certainly the rounding of the tuber may involve the floor of the cauline pit because it expands the pit. The beginning of the growth of the tuber is immediately after the cotyledon has driven the rest of the little plant through the hole in the seed-coats. Circumstances determine in which part of the hypocotyl it shall appear, two situations being debarred, namely the horizon of the hypocotyl where it passes nodally into the cauline pit and the similar part where it passes into the radicle. On account of this it must break out laterally somewhere between the two. By innate polarity it must be antithetic to the cauline pit; and it is driven to grow downwards by its geotropism. But it is a matter of accident which part of the globose seed lies uppermost in the soil and therefore it is a matter of accident in which direction the extruded radicle is thrust and whether the cauline pit faces upwards or downwards or in any lateral direction. Following the escape of the cauline pit from within the seed-coats, growth, intensified immediately under it, twists it upwards; and other growth in that part of the hypocotyl, whichever it be that is lowest, so long as it is in neither of the two debarred situations, begins the formation of the tuber. Should the radicle be below the cauline pit from the beginning, this growth will be in the region of x in Fig. 1A. Should the plant be upside down, it may be at y. It may indeed be in any position save transversely at the two debarred horizons. The plantlet is twisted into a correct attitude by these two happenings. Reference may be made to Fig. 2B (p. 317) of a seedling in which the base of the radicle and the petiole of the cotyledon were brought to positions at about 90° to each other by the extrusion of the tuber; and again to Fig. 3B (p. 319) for a like happening. These were simple cases and as such useful for enabling the more complex to be understood; but it is not planned here to describe them.

It is very unusual for the seedling to escape a large measure of twisting; and the twisting appears a clumsy manner of attaining a correct position; but it may be that the considerable resistances by the soil which have to be overcome, might not yield to a more delicate approach. The polarity is established on a new line, i.e. from cauline pit to apex of tuber; and the growing tuber thrusts the radicle aside. The radicle after this perishes; but not before two, or it may be three, roots of equal dimensions have grown from its base; but they perish with the radicle, whereafter every root on the plant is adventitious. Thus is *Tamus*, as many other monocotyledons, a plant which assigns all its business with the soil to the base of its stem; and as everyone recognizes, such specialization of the base provides important data in the classification of these plants; for it has been changed in many directions.

The reader will find pictured in Fig. 2 the radicle and the two lateral roots which have been pushed aside by the tuber, the enlargement of which has left them and the first leaf together.

The first contact of the radicle with the soil in germination cannot be otherwise than an occasion of great physiological alteration. Immediately after it mucilage appears in the tissues, both in ideoblastic reservoirs and in colleters; and the growth of the tuber would seem to find stimulation by it. There is of course no assimilation at this time.

Ideoblasts and colleters are of very general occurrence in the Dioscoreaceae, so general that a greater interest might be disclosed in finding them absent in any species than in finding them present.

Roots from the stem are in *Tamus* never from the annual stems arising from the tuber. Their restriction to the tuber is of interest, as they are produced readily enough from other parts in various species of *Dioscorea*. In the first place there are Dioscoreas with rhizomes on which roots arise. In the second place there are a few Eastern tropical species of *Dioscorea* well known to me which are able to throw out roots from the lowest nodes of their stems, particularly from underground nodes: and certain Madagascan Dioscoreas bear them, as figured by Jumelle & Perrier de la Bathie (in *Ann. Mus. Col. Marseille* (1910), sér. 2, **8**, 391 and 407). In the third place bulbils thrust out roots: they must do so or perish; the bulbils of *D. alata* at times do so before they fall from their parent plant. This power of initiating roots offers an interesting field for exploration. The power passes downwards on the tubers of *Tamus*; it wanes with age though apparently it is never lost.

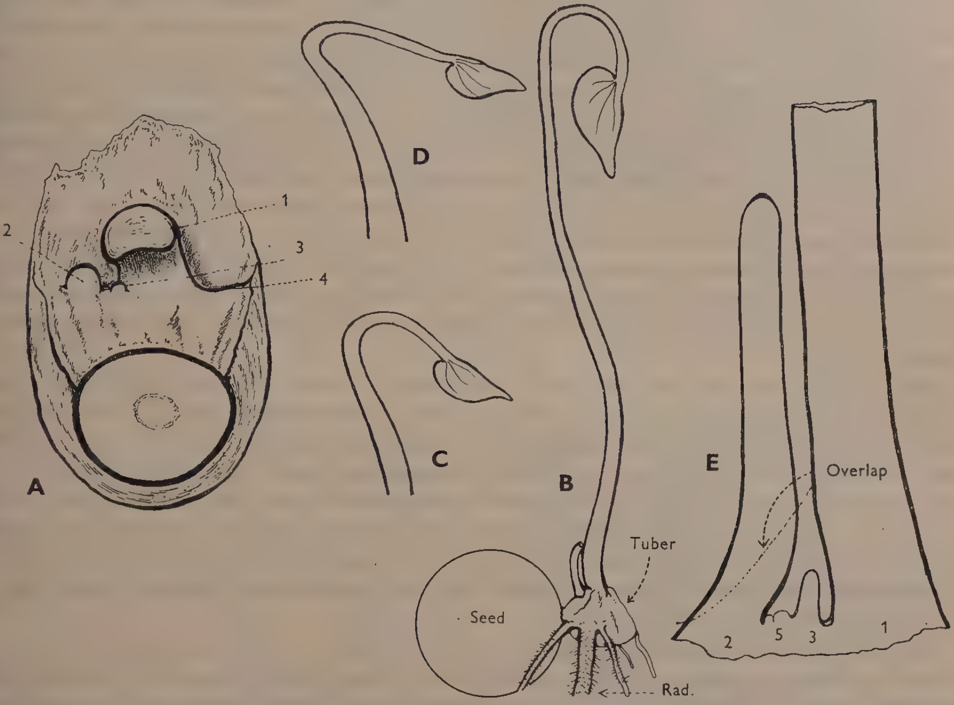


Fig. 2. **A.** The cauline pit immediately after germination, seen from over the petiole of the cotyledon which is cut through transversely, × 15. 1, its first assimilating leaf, growing upwards with the lamina bent forward on the petiole; 2, the second leaf; 3, axis; 4, a pit behind the first leaf. **B.** A seedling before its first assimilating leaf has reached the surface of the soil, its lamina bent downwards so that it is dragged upwards through to light, × 3½. The drawing illustrates one kind of twisting by which the cauline pit and tuber are brought to a correct position, the pushing aside of the radicle (Rad.) in the process and the origin of lateral roots from its base. **C** and **D.** Young leaves approaching the surface of the soil. **E.** A vertical section, taken near the end of the first season, showing: 1, the base of the petiole of the first assimilating leaf; 2, the arrested second leaf; 3, the apex of the axis; and 5, a bud in the axil of 2. The base of the first leaf overlaps the second making thus the brood-chamber.

I would have it well understood that there is very little in the seedling of the first season suggestive of a stem. The foliar organs are but little raised out of the cauline pit; the vertical section on the right of Fig. 2 shows a merely microscopic difference in level of the floor of the brood-chamber on the opposite sides of the axis, by no means indicative of an internode between the first and the second leaves; above that there is a short unfurnished apex. This inconsiderable axis carries the two leaves it bears at nearly 180° divergence (say 170° from the evidence in Fig. 3, p. 319). The brood-chamber is the tighter for the angle being near 180°; but the cause of this maximal angle is in the smallness of the axis.

3. THE SEEDLING STRENGTHENING ITSELF

The seedling of the first year loses the lamina of its only assimilating leaf before summer is ended, and with that withdraws underground to face its first winter, doing this with the base of its dying assimilating leaf clasping the base of its reserve leaf in such a way as to make a chamber for the protection of an axillary bud or it may be for the protection of an axillary bud to each of these leaves. One only of the two buds may be able to grow further; but it is not yet certain which is preferred, and, as observations on older plants indicate, the larger of the two buds may arrest the development of the lesser. Dr Agnes Arber (*Monocotyledons* (1925), p. 28) indicates a chance alternative at the base of the stem of *Orchis mascula* by these words: 'a bud arises in the axil of one of the lower leaves'; and in *Tamus* a choice between two is possibly not unusual, but no one has as yet worked out the directing conditions. Accompanying the protected bud or buds is the end of the axis standing centrally in the brood-chamber; but it cannot be described as protected, as it is dying. So die in later years the stems that come above ground. One postulates of *Tamus* that the habit of discarding its stems entered into the way of life of the plant because it could not preserve them through an adverse part of the year. But the stem of the first year is not carried above ground nor exposed; yet it is discarded while thus protected, though preservation would seem to offer an advantageous start in the second year. It has not shared the specialization of the tuber, but shares that of its own half of the plant by the working back into the seedling of this particular requirement of later years.

The bud that survives the first winter consists of a minute axis carrying a basal foliar organ which by disproportionate growth not only overtops the axis, but hoods it and envelops it; and as there is no internodal growth below, it is in immediate organic union with the tuber. This foliar organ, prophyll or scale-leaf, has as an obvious function the protection of the axis and must be classed with the coleoptile of grasses; but it never comes above ground as the coleoptile may. Its ability to envelop is the more easily attained because the axis is extremely small. Its specialization is such that it needs a distinctive name, and its shape is such that calyptrate or calyptriform scale-leaf or shortly calyptra is appropriate.

The axis carries colleters. It is usual to find in microscopic preparations that the chamber which the calyptra makes has been flooded by mucilage from their rupture; and manifestly in nature bruising and other causes of injury lead to such rupture and to the bathing of the axis in mucilage. This mucilage constitutes the fourth line of defence of the bud-tip; the first is the overlying soil; the second is the base of the axillant leaf in association with the leaf that follows in the form of walls of the brood-chamber; the third is the calyptra itself; and the last is this mucilage. In older plants the stem that has grown out makes one side of the brood-chamber, because it is so large in relation to the bud, the other being of calyptral origin; and this stem is hollowed slightly, the bud nestling in the hollow. The hollow is a slight exaggeration of a flattening present at the back of every axil on the plant (see Fig. 7). Every bud is given these four defences.

All Dioscoreas that have been examined have calyptrae: some of one form, some of another; some retaining greater power to continue growth than others; some thicker than others; some just closed and some very tightly closed; and some with a very little vasculation. That of *Tamus* is never vasculated. It is very much smaller and very different in shape from the scale-leaves that will be described in section 7 (see Fig. 8 on p. 326).

The lifting of the single assimilating leaf of the first summer to the light, as there is no stem, is the work of its petiole which has a considerable ability to elongate. I have induced it to elongate to 20 cm. (see *J. Bot.* (1937), p. 37) by robbing it of light, that is to say to a length out of proportion to the size of the lamina and much more than adequate to meet any normal need. The petiole ascends as vertically as a stem would, and, assuredly, is directed by negative geotropism. The cotyledon, this assimilating leaf and the arrested leaf which completes the brood-chamber, are all the foliar organs of the first season, spaced, as stated already, by nothing that can be called stem. In the second summer there is a stem; it bears a calyptra at its very base, a small scale-leaf and an assimilating leaf, after which there is a bud of small dimensions whereat the axis is arrested (see Fig. 3). In the third year the stem is not terminated with the abruptness of the second year; but there is the basal calyptra, then a short internode and a scale-leaf, almost always another internode and another scale-leaf; then the first assimilating leaf at the upper end of a longer internode; and this is followed by a short continuation of the stem with several leaves of diminishing size. The tip dies. This death of the bud at the end of a stem is hereafter a feature of stems, a character not connected with the annual death of the whole stem; the bud languishes, ceases to grow, and death follows sooner or later, the dying being limited downwards by a node, whereat a well-proportioned assimilating leaf occurs, healthy and effective in appearance. If this leaf be smaller than those before it, the diminution in size is only such as leaves towards the ends of stem show (for a contrast of the last leaf with the languishing bud, see Fig. 18 B, p. 341). Such death of stem-tips is not uncommon in plants, particularly in the monocotyledons, but too little attention has been paid to the conditions under which it appears, in spite of the fact that death is very important in phylogenetic speculations. As to the dying in *Tamus*, it has yet to be ascertained how the most closely related Dioscoreas behave before observations suggest the bearing of the dying of apices on the origin of *Tamus* from *Dioscorea*.

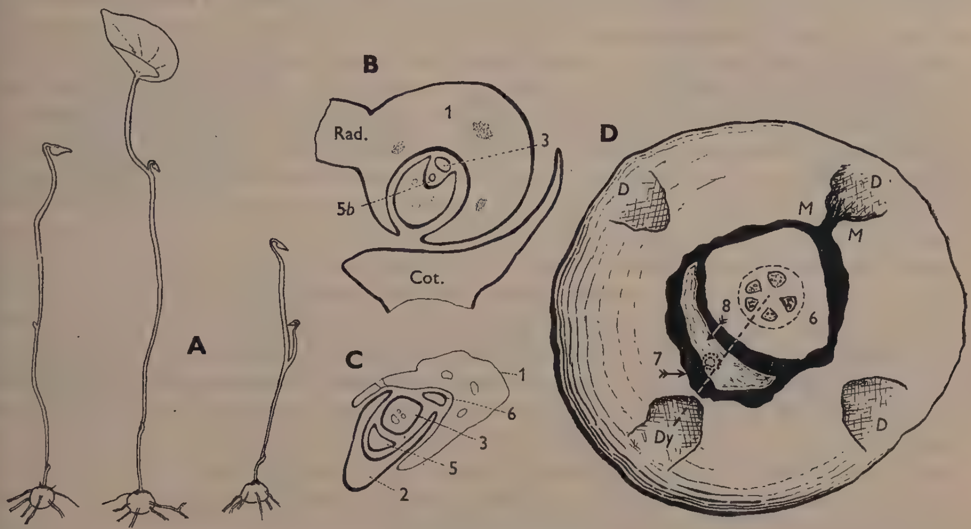


Fig. 3. **A.** Three plants at the beginning of the second summer, × 3½. Note the crook on the petiole under the lamina and compare Fig. 2, centre, and the swelling of the stems upwards. **B.** A section through the brood-chamber at the end of the first summer. **C.** A section through the same after the first winter at which time the bases of the leaves are dying: Cot., cotyledon; Rad., radicle; 1, the first assimilating leaf; 2, the second; 3, the end of the axis of the first summer; 5 and 6, cushions of tissue of the tuber which raise the axillary buds of 1 and 2. **D.** A section across the top of a tuber at the end of its second summer: 6, the stem of the year; 7, the bud laid down for the next year; 8, meristematic tissue in preparation for the bud of the year to follow; *D–D*, patches of decay from the lateral bundles of the leaf of the year before; *Dy*, ditto from the middle bundle; *M–M*, margins of calyptral pore.

This death, giving preference to a leaf in such proximity as to indicate self-pruning, does not represent preference in the matter of growth of leaf over stem, but of leaf over bud; for the action begins before the stage of stem-formation. It is observed that in successive seasons the distance from the base of the stem of the dying bud increases in what may be aptly called its strengthening; and the number of internodes can be used as a scale by which to express the strengthening. A supplementary scale of the early years is in the number of bundles in the axis at the base of which there may be three in an axis of the first year (Fig. 3 B), five in one of the second summer (Fig. 3 C) and so on until at maturity thirteen are expected.

In Fig. 3A it is shown that the petiole of the only assimilating leaf of the second summer is perched on the stem as if terminal, and that the stem is no greater in diameter than the petiole; moreover, the bud on the end is pushed aside. Sections in the position where the petiole is perched show that the radial arrangement of the vascular bundles in the stem is converted rapidly into the dorsiventral arrangement of a petiole with very little disturbance of the circumference, and that a large part of the conformity arises from the petiole being almost amplexicaul about a very small terminal bud. It cannot be without significance that stem and petiole are of almost the same diameter. But, as the figure shows, there had been an increase in the diameter of the stem from the base upwards to the diameter where it meets the petiole. On the upward increase of stems much will need to be said later.

These stems possess negative geotropism and ascend in the soil. I need now to show that there is negative geotropism in the tuber about their bases; it is of very limited extent, but, nevertheless, present in the immediate neighbourhood of the bases of the stems. It respects the polarity of the tuber. It makes itself evident in upgrowing lobes or cushions in and about the stem buds, which it may lift up, or it may engulf the bases. The positions of these upward growths suggest stimulation by the stem-buds. In Fig. 3C the cushions numbered 5 and 6 are such growths. The section there drawn was one of a series; and higher in the series the buds on these cushions were cut. In Fig. 3D is seen a crescentic body which, as other sections of its series show, is partly an outgrowth of the tuber and partly the calyptra of stem no. 7; the two are so united that it is difficult to lay down the line of union. Again much of the marginal tissue in Fig. 3D is the top of the tuber passing into the calyptra whose pore is indicated at *M–M*. Yet again in older plants than these, upgrowths intrude between the bases of overlapping calyptrae, and because their opportunities lead that way, begin the foundations for false keels. These do not ascend the calyptra in *Tamus*, but are somewhat developed in certain species of *Dioscorea*.

Such outgrowths show how permanently plastic the tuber remains.

It is convenient to describe Fig. 4A now, it being a section from a tuber of a plant still a seedling.

A tuber at the commencement of its fifth year was taken and the upper part cut into serial transverse sections. The outlines of these sections at a magnification of 28, were reproduced in layers of plasticine and a model built up by superposition of the layers. The figure made from the model shows the bases (3 and 4) of dead stems of the two preceding years; then (5) the living stem of the year. The everting effect of the growth had pushed 3 and 4 towards the margin and time had removed all trace of the calyptra of 3; but part of the base of the calyptra of 4 could be recognized. Stem no. 5, as the outcome of the axillary bud of this calyptra, obtained its surface of tuber by enlargement of the space between the stem no. 4 and its calyptra; followed by the bud for stem no. 6, and then again by the bud for stem no. 7, both being laid down long in advance of a need for them. The pattern that the everting growth produces is evident; it produces interstices which, at *y*, the tuber tends to fill. Fig. 4B–E give diagrammatically the geometric scheme of the building up. The sequence is evident with its pushing aside; and no explanation is required.

Later in this paper I shall illustrate responsiveness of the stem to stimulation from the bud as seen in the production of pediments.

Every old tuber has in its surface the dead steles of small roots sunk in pits. These roots had sloughed off their cortex, and the free space between them and the tuber had been occupied by it, and about it the swelling tuber grew. Many tubers exhibit also dead bases of aerial stems sunk in tissues that have grown up about them. The tissues hold the stems tight, and they are not in pits as the roots are: they are lobes of the tuber that have grown upwards. Brenner observed them (see Kirchner, Loew & Schroeter, *Lebensgeschichte d. Blutenpfl. Mittel-Europas* (1934) I/3, p. 695), and suggested that these lobes are produced by tubers that have sunk too deep into the soil, and that they serve to bring the head to a right depth. The suggestion is not exactly acceptable, for there is no exactly right depth that can be recognized; and the conditions that favour this upward growth are uncertain. Engulfing may hinder decay from penetrating into the tissues.

The very great specialization which on the one side prevents the base of the stem from ageing, keeping it as the perennial tuber, and on the other side provides an early death to the stems that are ventured into the air, is almost a family character of the Dioscoreaceae.

It is of phylogenetic importance that the early death is purposeful, even if, as it were, thrown into the way of life, and that it is not senescence.

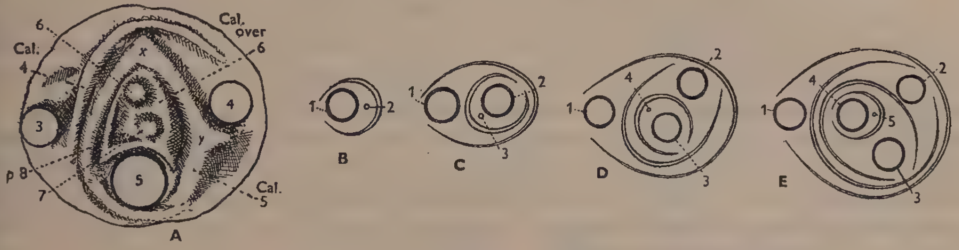


Fig. 4. **A.** The upper surface of a tuber in its fifth year with dead bases of stems of the third and fourth years numbered 3 and 4, the current stem numbered 5 and buds for the future stems numbered 6 and 7, all but the first and last with their calyptrae; *x* a keel at the mid-point of the calyptra of 5 and *y* an outgrowth of the tuber which would be a false keel if extended on to the calyptra; *p* 8, the position at which this further bud was in initiation. **B–E.** Diagrams giving the geometrical foundation of the sympodial ramification; axis no. 1 bears a calyptra and in the axil arises axis no. 2: axis no. 2 bears a calyptra and in its axil arises axis no. 3; lateral adjustments in accommodation follow.

4. The depth of the seed in the soil at germination and subsequent depth of the head of the tuber

Observations put on record in 1937 (*J. Bot.* (1937), p. 37) indicate that seeds of *Tamus communis* sink into the light soils that overlie the Permian of Devon on the average 4·5 cm. in the months before germination; and a maximum depth of 12·5 cm. was found. On heavy soils sinking is undoubtedly less as the resistance is greater and the quantity of water held by the soil is more constant. As the head of a mature plant is generally at a greater depth than the seed at germination, the tuber demonstrably continues the sinking. Gardiner & Hill (*Proc. Camb. Phil. Soc.* (1902), **9**, 445) attributed the sinking after germination to contractile roots; but no evidence has been obtained that there are such roots in *Tamus*. It is more likely that when the plant is small the straddled roots hold the plantlet down against soil expansions that follow rain in a way which leads to the soil being squeezed upwards between the roots, and that as the soil dries again, it and the little plant sink together. At a later age when the tuber is heavy, its weight holds it down against expanding soil; and the result is the same. Tubers have been found by no means infrequently at nearly 30 cm. below the surface; but on level ground it is unusual for them to be other than 10–20 cm. deep at the head.

In contrast to a depth of 30 cm. I have found the head covered by no more than the coating of leaves usual on the soil in a wood; but for tubers to be nearly exposed is so unusual that I shall indicate the nature of the conditions.

In a wood of coppiced hazel (*Corylus avellana* Linn.) on a clayey loam in Surrey with an overhead cover that was dense, I found a tuber wedged between hazel roots, which, whatever they had done when the plant of *Tamus* was young, at the stage when I found it held the tuber from sinking. In another wood where hazel was associated with holly

(*Ilex aquifolium* Linn.) on soil of the Reading beds, I found a tuber similarly situated. In a cove off Torbay in south Devon in scrub of *Prunus spinosa* Linn. just above extreme tide-limit on a black soil spread over fissured limestone I found a third tuber with its head exposed; it was one-stemmed and the stem dipped back from its origin into the soil before rising into the bushes at 15 cm. from the tuber. In each of these three cases survival manifestly depended on the density of the overhead cover aided by the litter of leaves that it made. So much for Brenner's theoretical correct depth. No doubt there is an optimum depth for survival in any locality; and apparently the physical conditions of the locality determine the depth by killing the unsuccessful. The amount of stem required to thread the overlying soil is usually that of two internodes.

5. WITH ITS STRENGTHENING THE TUBER ACQUIRES SEVERAL HEADS

It is a rule that a new stem is released from a single head when an old one is removed and the rule would keep the number of stems from a tuber constant, save when, now and then, two stems take the place of one by twinning (as seen in Fig. 7 D); but there is increase to their number brought about by the production of new heads around the original head. When a severe injury to a head destroys it, more heads than one appear in the neighbourhood; or even when a less severe injury arrests the original head, new heads appear and probably escape repression though the original head recover. Fig. 5 is the upper part of a multiple-headed tuber.

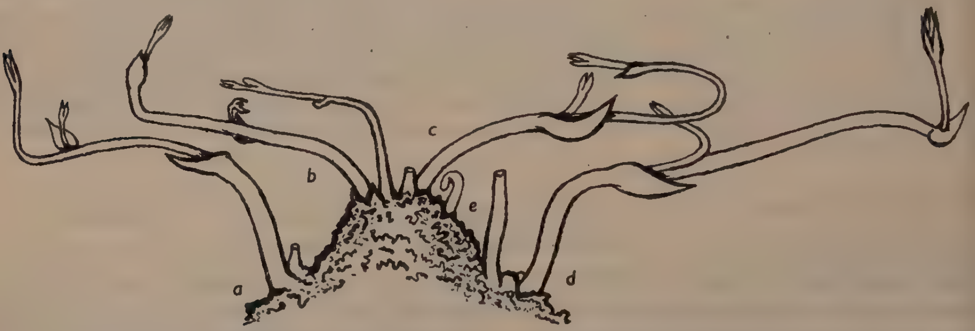


Fig. 5. The upper part of a multiple-headed tuber, typical of plants over six or seven years old, with the stems of early spring, *a*, *b*, *c*, *d* and *e*, and some stumps of axes of the previous year. × ½.

6. THE POWER OF THE TUBER TO REGENERATE NEW PARTS IS ZONAL

Tied up with the geotropic directing of growth in the tuber is the production of new roots; they are initiated in descending order behind the advancing descending growth, as inversely the opposite end of the tuber adds new heads.

In the spring of 1931 I took from the soil, where they had grown undisturbed from seed, a number of tubers of various ages up to about ten years; and after mutilating them in various ways, replanted them horizontally. From tubers that had been deprived of their lower ends, the new season's stems emerged normally as would be expected, and without delay. Out of those that had been deprived of their upper ends, the stem in renewal appeared a year later from a little under the horizon of decapitation. The lower end of the tubers did not bend down, but just away from the end, out of the surface which was downwards, grew a lobe replacing the natural end. The reader will observe that this shifting of the focus of elongation by way of adjustment is exactly similar to the happening in the hypocotyl when the newly initiated tuber shows itself as a lobe lateral to the hypocotyl. It may happen in such experiments as these that more than one lobe arises; but if a second arises it is invariably from the side of the tuber that has been caused to be downwards. My experiments have been briefly described (*Proc. Linn. Soc. Lond.* (1932), Sess. 144, p. 50). Leclerc du Sablon earlier had made similar experiments using very young material and had obtained similar results (see *Rev. Gén. de Bot.* (1902), **14**, 145–6). His experiments span with mine the first ten years of the life of the plant, and there is no reason to suspect a loss or change in responsiveness at any age. Some Dioscoreas have tubers that circumnutate; they could not do so were they not rather slender; and to the forbidding bulkiness of the apex of the tuber of *Tamus* may be attributed its adjustment of direction by lateral lobing. This, after all, is but a repetition of the behaviour of the hypocotyl in which an adjustable polar tuber-apex appears against a fixed polar cauline end.

The following experiment was done in a warm room in 1944–5. In September of 1944, a tuber 4 cm. long was cut transversely into three, namely a part with the head, a part with the lower end, and the middle with neither; and the three parts were placed on sand moistened with nutrient solution within a glass-covered receptacle. All three rooted with little delay; but the two headless parts took respectively twelve and six months to produce each a new head. The new head was produced in both towards the upper part of the fragment (see Fig. 6). When the stem from the head appeared, it bent itself into a crook as figured.

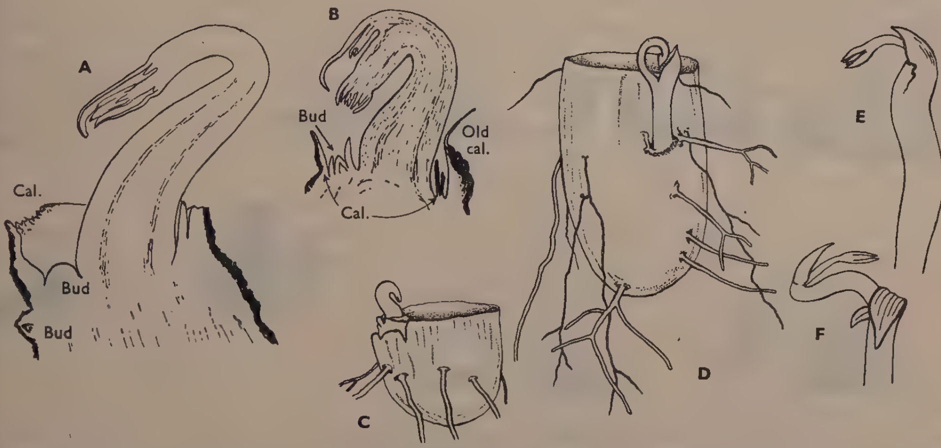


Fig. 6. **A** and **B**. Stems and the buds axillary to their calyptrae in vertical section, showing the stem bent into the shape of a shepherd's crook, with the convexity under the first scale-leaf after the calyptra; × 5. **C**. The amputated end of a tuber about ten years old with a regenerated head and a crook formed on the stem from it; nat. size. **D**. The amputated end of a tuber two full years old with a regenerated head and a crook formed on the petiole of the leaf from it; × 4. **E**. The stem from an uninjured tuber at a stage in growth when the crook has reached scale-leaf *A*, and the internode below it has straightened itself; × 2. **F**. The stem at a later stage with the crook transferred to the side of scale-leaf *B*; × 2.

In April 1945, four small tubers at the beginning of their third summer were decapitated and the lower headless part of each placed on sand in the same way. They, like the others, rooted promptly, and each furnished itself with a new head, but not until the latter part of September. One of the experimentally decapitated tubers with its new head is figured above (Fig. 6D). A short stem was produced, terminated by a single foliage leaf; and it was the petiole of this leaf that carried the crook, not the stem. A little ingenuity in experiment will be required to ascertain why crooks are on petioles in young plants, whether uninjured (Figs. 2 and 3) or after decapitation (Fig. 6D), and in contrast in older plants are on stems, whether uninjured (Figs. 6A, B, E and F; 7B–D) or after decapitation (Fig. 6C).

Winter weather, severe enough to destroy active heads, may cause a tuber to lie apparently dormant for a year, because new stems cannot be produced without the delay that the above experiments demonstrate; for instance, three months of frost at the end of the winter of 1946–7 caused some of my experimental plants not to appear above ground in 1947.

7. THE SCALE-LEAVES OF THE LOWER ZONES OF THE STEM

The calyptra is a scale-leaf of considerable specialization, never elsewhere than underground and never with an internode below it. It is widely unlike the rest of the scale-leaves. The line of decay, *d–d* in Fig. 7A, is inserted annually just above it as a major epigenetic boundary between the two halves of the plant. The underground position of this line has a relation to the calyptra; it is underground because the calyptra is.

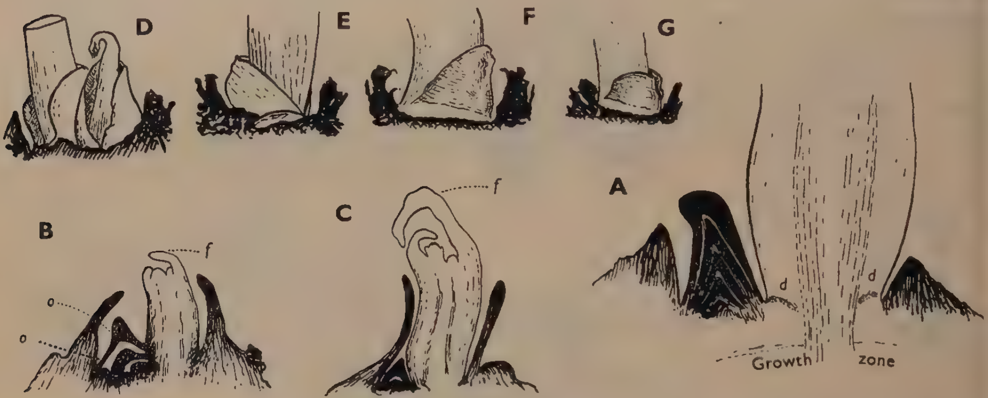


Fig. 7. A. A short vertical section through the base of a stem about to be self-pruned away, showing at the line *d–d* the first signs of dying; this line is immediately above the bud ready to give rise to the stem of the next year. B and C. Vertical sections through stems in October and early November in the plane of the bud for the year ahead, so cut as to show the hooding of calyptra over calyptra; *o* and *o*, the positions of pores of two of the calyptrae showing that by their different directions and possible different elevations the outer calyptra closes the chamber of the calyptra within it. D–G. Calyptrae which have retained their power to grow until spring, dissected free from the close packed bases of older calyptrae. D shows twinning which occurs sometimes; the two calyptrae face alike but one has outgrown the other. All × $2\frac{1}{2}$.

Though not a featured absciss line with precautionary cork, its position is predictable. It appears as a line of disorganization of cortical cells extended to the endodermis but not extending into the stele; and its time of appearing is the end of summer before there is any yellowing of the leaves. For four and more weeks from its appearance, a living stem, if pulled upwards by the hand until it breaks from the tuber, does so in the cortex at this line, but in the stele 1–2 mm. lower, the stele breaking within the tuber. On a stem left undisturbed the decay spreads upwards and a very little downwards and then through the stele, so that the life in the annual stem is at last cut off from the life in the tuber. Berries not yet ripe on the upper part of the stem continue to ripen. This dying with subsequent ripening of fruit is a widespread character also in the genus *Dioscorea*. Every foliar emergence on the stem of *Tamus* above this line of decay may be expected to top an internode. A few do not, and to this degree the condition of node without internode is achieved but not in the manner of the calyptra exactly. This suppression of internode occurs among assimilating leaves; but has not been seen at all among the scale-leaves above the calyptra.

The two figures 7B and 7C show the calyptra in the form of a bell-tent: Fig. 7A shows it taller. It may vary thus. It loses its power to grow in length, sometimes late so that it is not ruptured immediately the axis within it starts to elongate; more often it is burst open early. Having fulfilled its protective function it dies from the edges at a length of 2–5 mm. For the shapes of late-growing calyptrae see Fig. 7D–G.

To expose the calyptrae in the head of a tuber, the remains of old calyptrae must be removed, for they keep the close packing that originates in the sympodial bud. This close packing is protective to the tuber about its heads. The inner surface of a calyptra is smooth, even glistening. It is easy to identify its midline, partly by the folding, more by the even division on either side; then also by its axillary bud; but it has no vascular bundle.

Throughout the rest of this paper foliar organs will be identified by letters, so that one may be distinguished from another; and the internodes will be numbered. The first scale-leaf after the calyptra will be called scale-leaf *A*. It, although far less specialized than the calyptra, is peculiar in certain respects. It is much broader at the base than any of the scale-leaves that follow, but not so broad as to be amplexicaul. In breadth of base it is intermediate between the calyptra and the scale-leaves that follow it. It has generally five or seven nerves (see Fig. 8A); and in no other node of the whole stem is there a plexus of nerves so nearly deserving the name nodal plate, inasmuch as about three-quarters of the nerves of the stem at the node are involved. If it be right, and assuredly it is right, that the amplexicaul nature of the calyptra is promoted by the minuteness of the axis, so also is the approach to an amplexicaul base in scale-leaf *A* promoted; both are initiated early before the axis breaks open the calyptra; but emergence-initiation has wide time-intervals then; there is, for instance, a long interval between the production of the calyptra and the production of scale-leaf *A*; and it is prolonged, one might say artificially, by arrests that allow only one stem to exist in the head at a time; for there is again a relatively long interval between the initiation of scale-leaf *A* and scale-leaf *B*. Marching with these spacings in time of scale-leaf initiation goes a delay in internode extension, so that internode no. 1 which separates scale-leaf *A* from the calyptra, is for a time the only part of stem that exists (Fig. 6A). Scale-leaf *A* is initiated at a divergence of 180°, more or less from the middle of the calyptra. Not only is the amplexicaul base of the calyptra and the nearly amplexicaul base of scale-leaf *A* to be regarded as promoted by the smallness of the axis, but the maximal divergence of 180° is promoted thereby. It will be demonstrated later, that the divergence narrows as the axis by increasing in circumference offers more room for emergences.

Scale-leaf *A* shelters buds usually to the number three in column one above another, the first-formed uppermost. It is arched over these buds protectively, but is not hardened for that purpose, being wholly of soft parenchyma, including large mucilage-holding ideoblasts with raphides in the mucilage. These ideoblasts by expansion press apart neighbouring cells and become star-shaped with rays down the middle lamellae of the walls between the cells that they push apart.

It is normal for scale-leaf *A* to be underground, and there it remains white; but if it happens to be exposed to the light, a soluble pink or violet colouring matter appears along with a little chlorophyll. The pink or violet colouring matter is doubtless one of the substances discussed by Bartlett as in *Dioscorea bulbifera* Linn. (*Bull. U.S. Bur. Pl. Ind.* (1912), p. 264).

Scale-leaf *B*, i.e. the second after the calyptra, is 3-nerved (Fig. 8B), and narrowed from the base to the apex. If underground it is white as scale-leaf *A*, than which it is a little firmer. If exposed to light, it colours and has chlorophyll. Probably in its axil are three buds, as in the axil of scale-leaf *A*. It is usually raised as far as the surface of the soil.

Scale-leaf *C* is almost always carried above ground, and is the first of, say, four that are aerial and stand below the first assimilating leaf. They are all more firm than the subterranean leaves and hold chlorophyll, but are less green than leaf-green. In outline they make a progression towards the assimilating leaf in that there is a narrowing above the base (Fig. 8C and D) suggesting a petiole, and finally the outer pair of entrant vascular bundles branch (Fig. 8D), and a commissure may appear (see *J. Bot.* (1939), p. 328) such as is at the base of the petiole of an assimilating leaf. But the ultimate scale-leaf is still altogether unlike the first assimilating leaf. Scale-leaves should be defined by two qualities as being foliar emergences that are both arrested and turned aside: assimilating leaves are built into their autochthonous completion from that point where the scale-leaf meets with arrest. It is as if a catch in the apical bud has been slipped where the first assimilating leaf succeeds the last scale-leaf—a catch that was withholding freedom to carry foliar development beyond a certain point. Inasmuch as no differences in function are apparent between one and another of these aerial scale-leaves, it would seem that the differences that there are between them arise from an anticipatory loosening of the catch.

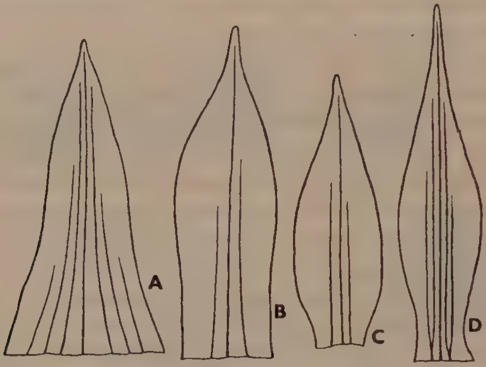


Fig. 8. Outlines of typical scale-leaves in order from below. A. The first after the calyptra and so forward. All × 3½.

These scale-leaves range from 14 to 22 mm. in length. The stem below ground has a thick parenchymatous cortex, which thins abruptly at the surface of the soil; and this suggests that the softness of the underground scale-leaves may be promoted by the humidity in which they live, as would seem to be the quantity of soft parenchymatous tissue in this part of the stem.

8. PEDIMENTS

By pediments I mean what Abbé Grégoire called 'sousbassements foliares', bracket-like supports of axial origin under leaves.

An internode of *Tamus* would be of even diameter throughout were it not for alterations which must be regarded as of nodal origin. At the lower end of an internode there is, as in very many plants, that slight flattening of the surface of the stem at the back of an axil which I have mentioned in section 3 (p. 318): it does not extend upwards for more than 1–2 mm. At the upper end of an internode, by a gradual enlargement over the leaf-trace, the circumference increases upwards to the petiole or to a scale-leaf; and this is the pediment. It causes a transverse section immediately below the node to be somewhat elliptic: as the pediment sinks downwards this elliptic shape passes away until a transverse section tends to be circular. The pediment causes short internodes to be stouter than long internodes if the shortness is such that its effect extends far enough. Its origin can only be in a factor which stimulates growth just below the leaf; and it can be added that this growth increases to advantage the surface requisite for carrying the furniture of the node, which furniture consists of (1) the petiole, (2) the axillary bud or buds and (3) the peculiar soft prickles that some botanists have claimed to be stipules

The words 'soft' and 'prickle', though essentially contradictory, in the expression very aptly express the nature of these unvasculated processes that are strewn about the stem of *Tamus* in pairs at leaf-bases; they represent the hard defensive prickles frequent in the allies of *Tamus* and in some very closely set along stem-angles near the ground, then gradually reduced in number to a pair at a leaf-base, when they finally disappear. *Tamus* never has more than a pair at a leaf and is very often without any at all. They are relics of ancestry and no more. It is common for them to be slightly bilobed at the tip; but very rare for them to be branched as was the one on the right in Fig. 9E. In the distal parts of stems, where they have become slender, the pediment may be called on to hold part of the vascular structures belonging to the node (Fig. 16, lower line). In brief the pediment is an accommodation.

At the initiation of a node the axillary bud is situated on the face of the stem just above the leaf-base; along with the enlargement of the adjacent part of the stem, it is carried out on the pediment and then looks as if it were on the petiole; and the soft prickles are carried out also, by which their illusory resemblance to stipules is increased. The accommodation of multiple buds is facilitated by the enlargement of the pediment as in Fig. 9A, B. In Fig. 9A the result of an experiment is recorded; the parent stem was decapitated and the senior bud thereby liberated for growth, growing into a stem as stout as was the parent. In Fig. 9B lesser damage to the apex of the parent stem was produced which checked but did not destroy it, whereon the senior axillary bud was released in a competition that did not allow it to attain the size of the parent. In both these figures very considerable enlargement of the pediment occurred, and in its growth it carried outwards the axillant scale-leaf. Fig. 9D represents the result of repeating the decapitation on the stem that had replaced the parent. Still greater enlargement of the pediment resulted from this. And no one will deny that the stem just below the node shows itself liable to have its growth increased by a demand for space for attachment areas for the axillary buds. Fig. 9C shows that the relation of an inflorescence to the parental stem is as the relation of the vegetative branch in Fig. 9A, B and D.

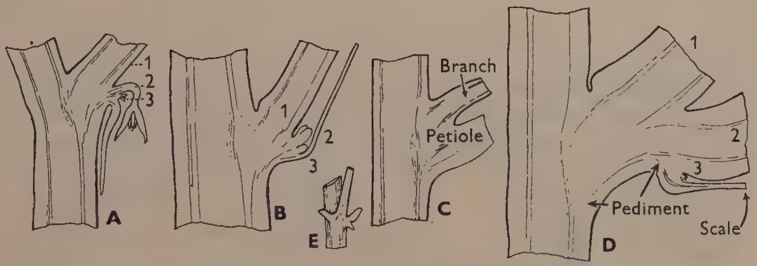


Fig. 9. **A**, **B** and **C**. Normal pediments: **A**, from underground; **C**, from the horizon where inflorescences were in the axils, showing the insertion of the base of a panicle. **D**. A pediment stimulated doubly to grow, first by the amputation of the apex of the parental stem, then of the apex of the first replacing stem. The multiple buds or the stems from them are numbered 1, 2 and 3 in their order. Note the carrying outwards of the axillant scale-leaf. All × 2½. **E**. The base of a petiole with soft prickles on the pediment, one of them abnormally branched.

There is a curious development in the section *Lasiophyton* of the genus *Dioscorea* which shows the pediment in a light other than as the spatial accommodation which it is and no more, in *Tamus*. In the male inflorescences of, for instance, *D.* (*Lasiophyton*) *kamoonensis* Hook. f., the flower is covered by the bract in the axil of which it originated, and the two are carried out on what is called a pedicel in descriptive work. That pedicel is an exaggerated pediment. Theoretical morphology which calls it pedicel and bract in fusion is at fault in doing so.

9. THE BENDING OF STEM OR PETIOLE INTO THE FORM OF A SHEPHERD'S CROOK AND THE BEHAVIOUR OF THE STEM ON ITS WAY TO THE SURFACE OF THE SOIL

Comment has been made (p. 323) on the bending of stem or petiole into a crook in the forcing of a way through the soil. The crook is produced by stronger growth on one side than on the other; and the side of stronger growth on the stem is that of the foliar organ immediately over the crook. Scale-leaf *A* being more or less at a divergence of 180° from the mid-point of the calyptra, the terminal bud is thrown to the calyptral side (Figs. 7 B, C; 6 A, B). This can be understood if it be held that scale-leaf *A* stimulates the tissues immediately below it to a growth which bends the stem, doing this by means of a hormone, the path of which is from the scale-leaf down the leaf-trace, and that this hormone becomes used up by the tissues that are most ready to respond: then because the condition of responsiveness travels up the stem, so does the crook, orthotropy behind it straightening the crook out. It remains for someone to prove the presence of the hormone by extracting it.

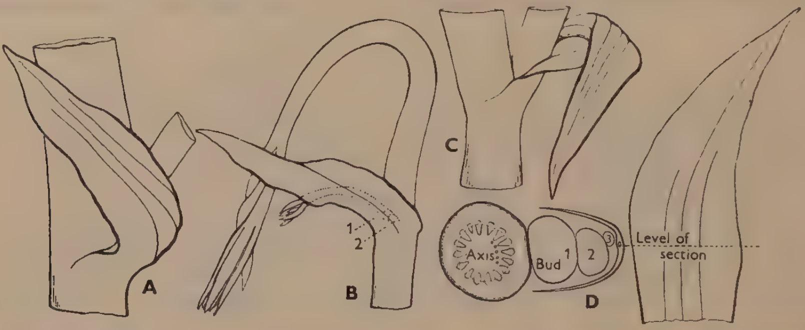


Fig. 10. The bending of the scale-leaves to one side. **A** and **B**. Normal inclination showing (in **B**) that its direction is the direction of the crook. **C**. A scale-leaf which has been bent down by friction with the soil (cf. also Fig. 9 **A**). The axillary shoot is bent also. **D**. An inclined scale-leaf and the furniture of the axil showing that the inclination cannot arise from a mechanically induced drag by the axillary buds. All × $2\frac{1}{2}$.

The crook comes into being in the darkness of the soil. It reaches scale-leaf *A* in due time (Fig. 6 E); then the condition of responsiveness passes the node of scale-leaf *A* and the stem is flexed into a crook from scale-leaf *B*. But scale-leaf *B* is at a wide divergence from scale-leaf *A*; so the crook is either thrown right across the stem (Fig. 6 F) or caused to sidle round it. When responsiveness ascends in the stem beyond scale-leaf *B*, the crook persists as a nodding of the end of the stem, where, instead of only one internode being involved, there is a less striking extended curvature towards which more than one foliar organ is in a position to stimulate flexure, and the effects intermingle, but in a way that cannot yet be fully explained.

The bending of a petiole into a crook (Fig. 2 B) may be regarded as brought about similarly by a hormone from the lamina acting on the most responsive part of the petiole; the flexure follows. The hormone would originate in the leaf-tip, as leaf-tips in other plants are proved sources of auxin. In an account of leaf movements in *Tamus* (*Proc. Linn. Soc. Lond.* (1944), Sess. 155, pp. 252–77) I assigned (p. 255) the unfolding movements of the petiole of assimilating leaves of mature plants to auxin from the leaf-blade; and I hold it as probable that these petiolar movements are less spectacular exhibitions of the work of that auxin which brings into being the underground crook.

With reasons for believing that every foliar emergence on the annual stem has these secretions, bud-protection ceases to be the only recognizable function of scale-leaves; as, if they are necessary for controlling growth of the stem and if, as is more than likely, remoteness is an inconvenience, the dispersion of scale-leaves in series over zones not served by assimilating leaves is a key to success. Then it follows that the buds in the axils, being obviously of little service, are retained in their positions because the scale-leaves are there and are consequential on the need of the presence of these.

Because the stem while underground develops leisurely, the time-lag of scale-leaf *B* after *A* ensures that there shall not be conflicting crooks.

Granting that the crook saves from injury the emergences when they are very tender it is at the same time inefficient when it fails to prevent scale-leaf *A* from being folded back out of position by the resistance of the soil. This scale-leaf, and also those that follow, have a property which causes them to incline to one side (Fig. 10A, B) in an inclination which renders them definitely exposed to further bending from soil-resistance than if they were straight; and they may be bent by it (Figs. 10C, 6F), even so completely as to be inverted (Fig. 9A); but this last happening is rare. The tendency to incline to one side enters also the axillary bud so that it too inclines as it forms a stem (Fig. 10D). The horizon in the scale-leaf at which the curvature causing the inclination takes its maximum effect is well above the base, and the curvature cannot be due to a mechanical drag from buds in the axil. Fig. 10D demonstrates this. The inclination looks as if disadvantageous, though it may in rare cases prevent the glandular apex from premature destruction.

10. THE GROWING OUT OF THE STEM INTO THE LIGHT

The stem on arrival in the surface soil has its negative geotropism overcome and bends horizontally; but the crook is retained, its position being well above the bend. The cause of the bending is therefore not that which creates the crook. The crook even appears tightened (see Fig. 11A, D); but that is from the increased length of the apical part. It tends to lie flat against the surface; while the stem pushes it forward among the leaf-litter and the loose surface soil for 10 cm., or more, before, on its opening out, the stem resumes an upward growth. In this upward growth the stem inclines from the light and so towards bushes, etc., that may later be twined on, though twining does not begin at once. If the plant be on a bank, it inclines towards the surface of the bank. Its behaviour in this is like that of *Galium aparine* and is purposeful. Only a few days pass before the crook opens out (Fig. 11A, B); but the bend which renders the stem horizontal remains and deploys advantageously the multiple stems of an old tuber so that they may twine in their ascending where they are less likely to twine on each other. On the whole the more shallow the soil in which a plant grows, the greater the deployment. Fig. 11F illustrates this, representing a plant from rubbly soil into which, on account of the stones,

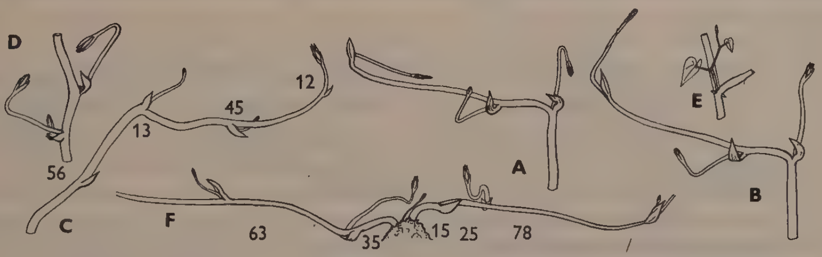


Fig. 11. **A.** A stem in mid-March which having ascended under negative geotropism became at the surface of the soil horizontal, the branches also horizontal, their crooks flat. **B.** The same a fortnight later, the stems now growing upwards and the crooks opening. **C.** A stem showing that the flexures are greatest near nodes; the numerals against the flexures give the radius of the curve at the point. **D.** The horizontal part of a stem seen from above showing flexures at the nodes and crooks horizontal. All $\times \frac{3}{10}$. **E.** A weak axillary branch from the upper part of a plant showing that such also have flexures at nodes. **F.** The head of a plant from very shallow soil, illustrative of the deployment produced, the numerals are the lengths, in millimetres, of the internodes to which they are adjacent.

the tuber could not sink. Earlier in this paper (p. 322) attention was called to the way in which a stem from the exposed head of a tuber dipped under the soil and did not ascend for 15 cm. There were no additional stems from that tuber; but its only stem acted in accord with the manner in which stems deploy.

Orthotropy does not remove these flexures as it removes the crook. They extend both above and below a node. The sharpest is where the stem emerges from the soil (Fig. 11 A) and turns the stem away from the scale-leaf. All these curves indicate stimulation about an axil—a stimulation which differs, possibly in causation and certainly in effect, from the stimulation which enlarges a pediment.

Weak axillary branches, such as are not uncommon among the assimilating leaves, show comparable flexures at nodes (Fig. 11 E); but stronger branches do not. The difference doubtless begins in the size of the bud: if it be vigorous there would be conflicting influences on different sides; but if it be small and the influences weak enough not to overlap, each stimulation to bend might escape interference. Is it possible that at the time of the escape of the stem from the soil there is also an escape from interference, in this case resulting from the abrupt entrance of the one stimulation?

11. ZONATION OF THE STEM BY THE SERVICES DONE

In the Surrey hills, where most of my observations have been made, a mature plant of *Tamus communis* carries fifty and more assimilating leaves on each annual stem. To carry fewer is in general a mark of immaturity. The stem at maturity is 3 m. long or more; the longest so far met with and measured was 4¾ m. long. The greatest number of foliar organs, scale-leaves and assimilating leaves together, was 110. Function suggests the following five zones:

TABLE 1. *Zonation of a stem by function, from above downwards*

Zone no.	Its features	Its service	Its depth in nodes
V	♀. Assimilating leaves with axillary inflorescences	Reproduction with assimilation	Up to 50
	♂. Ditto	Ditto	Up to 100
IV	♀. Assimilating leaves with axillary buds of vegetative potentiality	Assimilation	10–40
	♂. Ditto	Ditto	1–25
III	Scale-leaves with axillary buds of vegetative potentiality	Raising the above to better light	Usually not more than 7; say 4–5
II	Ditto, but underground	Driving the apex of the stem to the surface	1–3; usually 2
I	An abundantly protected sympodial bud, added to by one scale-leaf at a time	Perennation	1

These zones may be called: (V) the fertile assimilatory, (IV) the infertile assimilatory, (III) the zone of the spring push, (II) the underground zone, and (I) the perennial bud. The spring push is characterized by very rapid elongation, whence the name adopted.

I have already explained my adoption of letters to denote scale-leaf *A*, scale-leaf *B*, and so on. Though by using letters to indicate the horizon of every foliar organ, the alphabet is run through four times when a stem bears so many leaves as that of *Tamus* can, the reader will not find himself confused because I rarely need to particularize in regard to emergences after the earlier. The internodes by number are: internode no. 1 is that below scale-leaf *A*; internode no. 2 below scale-leaf *B* and so on.

The stem of *T. communis* does not taper from its base; but, after being relatively thick underground, abruptly thins at the surface of the soil, then increases upwards to a maximum circumference and diminishes to the distal end. The thickness underground is in the cortex. It appears right, for the reason that the cortex suddenly becomes thin where the stem emerges from the soil, to maintain that its thickness is promoted by physical conditions within the soil.

The greatest circumference of the stem is in zone III.

As in every axil buds occur, at least one and sometimes two or three, they are so numerous that any well-grown plant is likely to have upwards of 100 and may have more. In the number above ground there seems to be a wasteful prodigality. All that are between the calyptra and the commencement of zone V are bound in apparent uselessness by apical dominance, from which they are liberated for growth only if the apex of the stem be destroyed or extensively damaged in late winter, or spring. In time the apex dies and therefore can no longer exercise dominance, but before this happens the buds have lost their responsiveness. The buds of zone V are reproductive and not bound. Vigorous vegetative branches may be caused to grow from buds immediately below the lowest inflorescences, which shows that the transition to fertility from vegetativeness is abrupt and the apical dominance binding up to the very axil at which fertility begins.

In England it is extremely common for buds in the axils of scale-leaves *A* and *B* to be released for growth, as frosts are very destructive to the apices of the stems before or at emergence from the soil. But these frosts very generally spare the buds in the axil of scale-leaf *A* and generally those in the axil of *B*, probably in no way because they have a greater resistance, but because, being deeper in the soil, they have more protection. A replacement is made from the oldest of the buds in either axil, in that of *A* if there has been injury in that of *B*, or in that of *B*, as nearer to the apex, if there has not been injury also to *B*. To say nearer to the apex, means nearer to a condition of growth characterizing the apex. Very late frosts, such as may occur after the axil *C* has made the necessary advance, and particularly should *C* happen to be underground, lead to it replacing the lost apex; but this is uncommon, both because such frosts are not common and because axil *C* is generally above ground. From a cause that is not understood, replacements from underground attain the dimensions that the destroyed parent would have had, and replacements from above ground are smaller (see section 20, p. 372). Buds from *D* upwards are so seldom called on to replace lost stems as to possess no reason for existing to replace.

The zonation of Table 1 extends into the branches; a branch from scale-leaf *A* completes more or less the complement of scale-leaves due on the parent before it produces assimilating leaves. A branch from scale-leaf *B* may be expected to produce one scale-leaf less. A branch from one of the uppermost scale-leaves begins with assimilating leaves. There is a little inexactitude; but the zonation is present. On a sufficiently long branch fertility appears (see also p. 373). Inflorescences are not smaller on branches from below ground than they would have been on the parent; but they are decidedly smaller on aerial branches.

Weak branchlets as in Fig. 11 E are by no means uncommon: because of their smallness they are frequently overlooked. Possibly a slight damage to the apex liberates them for growth; if so, apical dominance has degrees.

Male panicles may be of considerable size, attaining even 40 cm. in length on the main stem; but a vegetative branch from the axil just below the lowest panicle can exceed this.

Twining is zonal in that it does not occur below the assimilating leaves. Branches twine likewise from the horizon where they become leafy.

It has been mentioned that the scale-leaves make a gradient towards assimilating leaves in shape and vasculation, though their final displacement by assimilating leaves is abrupt. It must now be added that the series of assimilating leaves does not commence with leaves of the largest size. This is indicated by the few measurements shown in Table 2, and any hedgerow where *Tamus* grows will provide further illustrations. After the largest there is a long gradient to the most distal.

At least half of the assimilating leaves on a stem are initiated in the dark of the soil under physical conditions little differing from those under which scale-leaves are initiated. The annual cycle determines the change-over.

TABLE 2. *Lengths in millimetres of the laminae of the lowest assimilating leaves of a few stems taken more or less at random*

1st	2nd	3rd	4th	5th	6th	7th
18	28	36	37	37	39	40
42	49	78	84	81	95	101
56	65	70	77	78	84	91
63	71	74	72	65	79	78

Flowering enters into the behaviour of the stem at different levels in the opposite sexes, with the exhibition of the first inflorescences being slightly under maximum size as are the first assimilating leaves.

The following gradations lead to the final cessation of growth at the distal end: (i) the diminishing of the circumference of the stem; (ii) the shortening of the petiole; (iii) the diminution of the superficies of the laminae; (iv) the contraction of the inflorescences by fewer branchings, whether they be male or female; (v) almost *pari passu* with the diminishing of the circumference, a reduction in the width of the vegetative line across the axil; and (vi) accompanying this a narrowing of the divergence. In contrast the size of the flowers shows no notable reduction, nor the size of the berries. So there are two kinds of reduction towards the distal end, in the one the lessening supply of material is matched by the production of smaller units; in the other by fewer units. The latter attain completeness, it may be said, autochthonously.

12. INTERNODES

Though internodes, because they are intercalations between the nodes, are secondary in time and are in their simplification of secondary importance, it is convenient to set down sundry particulars regarding them before setting down the character of the nodes. In the first place they, in *T. communis*, are exceedingly variable in length (see statement on p. 365), measuring from almost half a metre to nothing at all; and though it is easy to observe that their dimensions diminish towards the distal end of the stem and also that the first few are characteristically short and are followed by others that are characteristically long, and to observe as well that their average length is connected with zonation, there is an appearance of disorder in their elongation in each zone. Nevertheless, there is actually a large measure of order. Length of internode and measure of circumference being correlated in a broad way, it is growth rather than length which has the seeming disorder.

All internodes above ground are ridged down their surface, the number of ridges being in near relationship to the circumference and therefore also in relation to their lengths, though so loosely that the relationship is not evident until it is expressed in averages. The thick cortex obscures ridges underground. Above ground the epidermis of an internode is even over ridge and groove. The epidermal cells are as broad as deep; they are elongated in the direction of the elongation of the internode. Their outer surface is not flat, but slightly convex in a way probably useful to a climber by preventing slipping over the stem climbed on. In contrast to the stem the lower surface of a leaf is found to be absolutely smooth. Stomata occur on the stem in the grooves of the internodes. The ridges of the stem are built out by bands of collenchyma (Fig. 12A). Ideoblasts lie in loose columns down the ridges; the smaller of them tend to taper at opposite ends and are always elongated in the plane of the internode. The larger tend to be brick-shaped, and are similarly orientated. Cortical parenchyma, with stomata, comes to the surface of the stem in the grooves between the ridges, and the long axis of each stoma, like the epidermal cells and the ideoblasts, is in the long plane of the internode. This cortical parenchyma is without intercellular spaces, and its lowest layer has enough of the characters of endodermis to deserve this name; it abuts on a pericycle inwards against which the vascular bundles rest (Fig. 12 A). The bundles are of two rings, an outer ring under the ridges and an inner ring under the grooves. There is little difference in the depth from the surface of their setting; but the larger (alternate) bundles extend deeper. In some species of *Dioscorea* there are two very distinct rings of bundles, one decidedly outside the other; in *Tamus*, with but little difference in depth, there is yet no difficulty in recognizing two rings. The necessity for names for them is conveniently met by Hanstein's terms, 'common' and 'cauline'. The first are those common to the stem and the petiole, and three of them enter each leaf-trace; the others do not pass into the petiole and are 'cauline', as confined to the stem; and two of them belong to each leaf-trace. I have devised for this paper a way of representing their connexion with the leaves and used it in the diagrams from Fig. 34 forward. Beauvisage (in *Bull. trimestr. de la Soc. bot. de Lyon*, nos. 3–4, p. 78: 1888) somewhat earlier than Hanstein had, equally appropriately, called them 'valleculaires' and 'carenaux'. Queva (in *Mém. Soc. Sci. d'Agric. et des Arts de Lille*, sér. 4, **20**, p. 100: 1894) called them 'massifs sortants' and 'massifs reparateurs'. The two, 'common' and 'cauline', generally alternate; and where they do not, it is because two common bundles run side by side. Two cauline bundles never do this. When the numbers are equal the arrangement may be described as exact pectination; and this is common in many species of *Dioscorea*. Exact pectination is rare in *Tamus*.

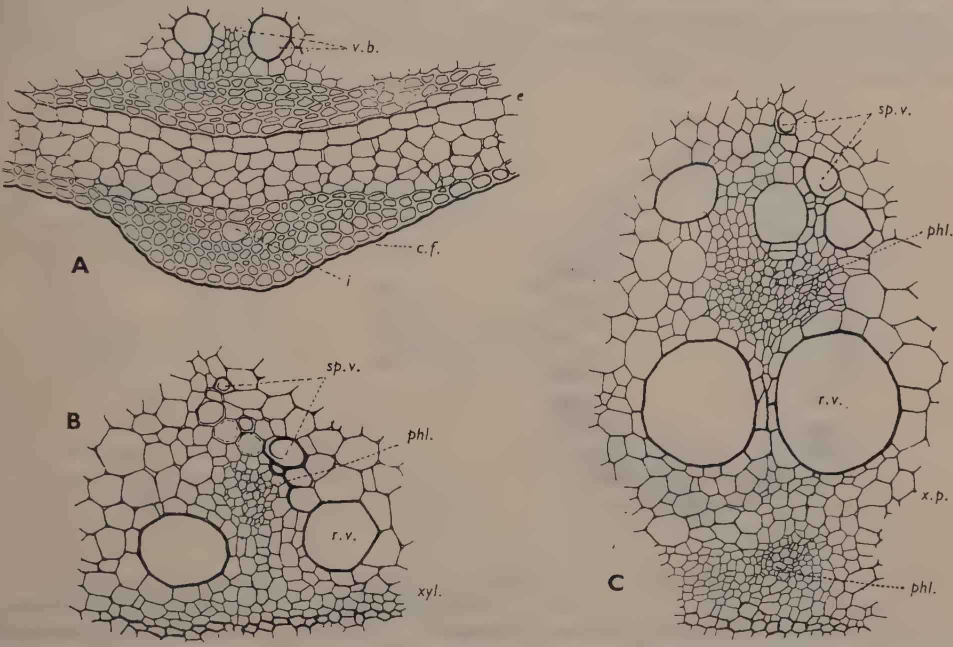


Fig. 12. **A.** The ridge of a stem in transverse section: *c.f.*, cortical fibres in the middle of which is an ideoblast (*i*) holding raphides in mucilage; *e.*, endodermis but without all the characters of an endodermis; *v.b.*, the margin of a vascular bundle. **B** and **C.** Typical vascular bundles, **B**, a common bundle; **C**, a cauline bundle. The greater size and double nature of the second should be noted: *sp.v.* spiral vessels of the protoxylem; *r.v.*, reticulated vessels; *phl.*, phloem; *xyl.*, xylem; *x.p.*, xylem parenchyma. All ×80.

Fig. 12 B, C give all that is necessary here of the structure of the bundles. The reader may be referred to Bucherer's paper in *Bibliotheca botanica* (Heft 16, 1889) for additional information. Von Mohl in 1845 (*Vermischte Schriften, Ueber d. Bau d. Palmenstammes*, p. 149) pointed out that the cauline bundles are compounded. Bucherer agrees; and I find them in development to arise from a double provascular strand, and occasionally in the

stem to break into two. Of this more later. The halves do not need names for they, except under very rare circumstances, behave as one bundle.

Nägeli inserted into his *Beiträge zur wissenschaftlichen Botanik* (1858, pp. 124–8) an account of arrangements which he had observed and, under the impression that the axillary bud drew its vasculation direct from cauline bundles, called them axillary: this was wrong. He went to great pains to show the up-spiral and the down-spiral side in a leaf-trace to differ; but he was curiously unfortunate in limiting his material, so that while discovering great variability he did not discover how the stems varied. Further reference to his account is unnecessary.

The invariable position of common bundles under ridges means that by counting ridges the number of common bundles can be ascertained; but as the cauline bundles are almost always fewer by a varying number, the exact number of bundles is not to be ascertained by this counting.

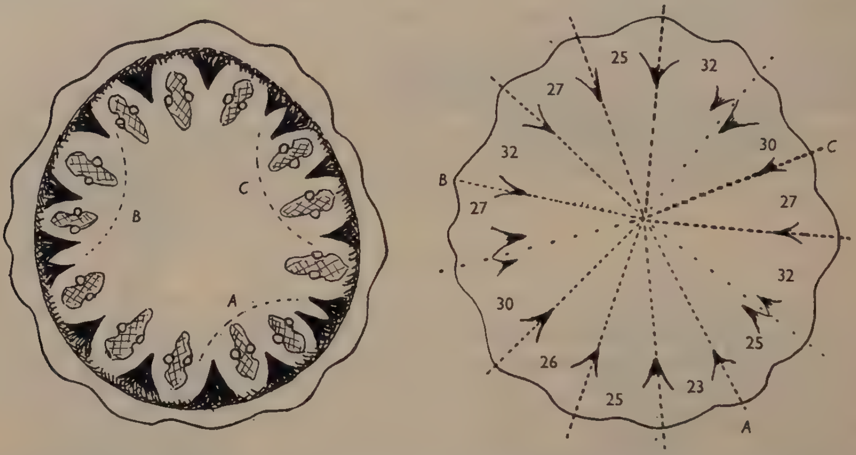


Fig. 13. Camera-lucida outlines of a transverse section through an internode at mid-length with the positions of the protoxylem of the common bundles accurate and (right) the divergences between them measured. The bundles bracketed together as *A* are the leaf-trace of the leaf immediately above the internode; as *B* of the next higher and of *C* of that following above. They were the 14th, 15th and 16th foliar organs of the selected stem.

It is easy to identify the ridge of the mid-common bundle of a leaf-trace at the horizon of the pediment, and possible, though sometimes only with patience, to trace it to the lower limit of the internode and ascertain how many ridges separate it from the mid-common of the next leaf below. Let us assume that we find it to be five and then by a section of the stem or other means we find that the total number of ridges, i.e. of common bundles, is thirteen. The divergence thus worked out is 5/13 or approximately 138·5° of the circle. I use this way of ascertaining divergences and I see no vitiating inaccuracy in using the results for my purpose. To explain it, Fig. 13 has been prepared. A section was cut at the mid-length of an internode, then drawn under a camera-lucida at a magnification of 28 diameters, care being taken to fix the relative positions of the protoxylem (inner angle) of the common bundles with accuracy. This drawing is the source of Fig. 13. The centre of the section was determined as nearly as possible; radii through the protoxylem of the bundles were superposed and the bundle-divergences measured on them. Fig. 13B gives these divergences as far as required. This stem had sixteen common bundles and thirteen cauline bundles, a not unusual combination, twenty-nine in all which, if exactly equidistant, should diverge at 12·4° from each other, or one common to another common, say, 25°. This angle of divergence occurs in the figure, but the equidistance is somewhat disturbed by the pairing. However our business is not with bundle-divergence, but with leaf-divergence. A glance at the figure suggests that the irregularities of bundle-divergence are so distributed round the stem as to cancel one another's irregularities out when the larger units of leaf-divergence are measured. I leave the data in Fig. 13 B with the reader, claiming that my method of work is reliable for the purpose in hand. But it is seen that two common bundles, when running paired, may be very close to each other. Cauline bundles keep good equidistance.

A bundle is not always of uniform diameter throughout its course, but often tends to diminish downwards. This is easily seen where bundles that descend into the tuber behave like rivers that sink into sands; but it can be seen also in the stem. Two conspicuous cases of diminution are illustrated in Fig. 14 in camera-lucida drawings of sections selected from a series cut through a terminal bud. The first of these is a transverse section cutting the axis below the horizon at which the foliar organ *F* would be freed; and the evidence of diminution is in Fig. 14 B and C, each successively 800 μ higher. Attention must be drawn to certain details of these figures and the diminution pointed out.

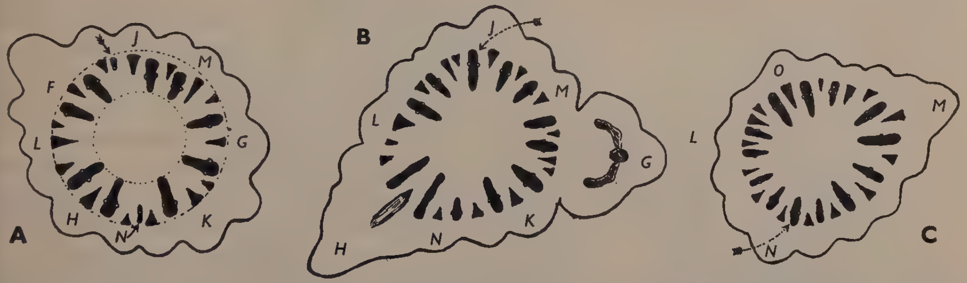


Fig. 14. Camera-lucida outlines of sections through an apical bud taken in very early spring. The sections are at successive horizons about 800 μ apart. The letters on them indicate the leaf-traces and are set against the mid-common bundle of each trace. **A** is through the bud just below the emergence of foliar organ *F* and naturally all five bundles of the trace are present. **B** is at the horizon where foliar organ *G* was freed. **C** is just below where *M* is freed. The dotted circles in **A** are only a guide to the eye inserted for the purpose of demonstrating that the distance of the bundles from the centre is not quite constant.

Fig. 14 A shows towards its upper side on the left the cortex thickened as a pediment over the leaf-trace of *F*; the bundles of the leaf-trace have not been spread as yet out of the ring. Thus it is evident that the increase of thickness by which the pediment is formed is cortical only. On the right of the same figure the emergence of foliar organ *G* has also made its effect, and the position of foliar organ *H* is indicated below. It will be noted in regard to them that the mid-common bundle of each leaf-trace is rather larger than either of its neighbours and that there is a difference in size between the lateral common bundles, for the up-spiral is larger than the down-spiral. The leaf-traces of these three foliar organs, each of five bundles, account for fifteen of the twenty-six in the double ring; leaf *J* claims four of the remainder, *K* three, *L* one, *M* two and *N* one. This was proved by tracing the bundles upwards through the series of sections. In order to descend to the horizon of Fig. 14 A the bundle originating with *N* had passed through seven internodes: it had one more internode to pass through before extinction. Attention is drawn to its small size in Fig. 14 A and its larger size at the higher horizon of Fig. 14 C, as indicated at the arrow in that figure.

One of the bundles in the leaf-trace of *J* had been extinguished above the horizon of Fig. 14 A, two of *K*, three of *M* and four of *L* and *N*. The manner of extinguishing is demonstrated in section 17 of this paper (p. 359), and the number of internodes that different bundles thread is explained. Here it remains to note that by no means all bundles suffer the diminution seen in that of *N*; for instance, other bundles of the same leaf-trace suffered no diminution after the immediate neighbourhood of their origin. The circumstance that in this stem *M* was represented at the horizon of Fig. 14A, by two bundles, but *L* (less distant) by only one, warns the student to expect irregularities. Another bundle which showed loss of size downwards came from foliar organ *J*. Both bundles cited for loss of size were down-spiral cauline bundles. One of them is enlarged in Fig. 15A.

It has been stated (p. 333) that the cauline bundles are compounded of two. Some diminished bundles have lost one-half; they include only one phloem group instead of two (as in Fig. 12C). The halving is in certain cases a consequence of part of the bundle becoming confluent with other vascular tissue in the manner of Fig. 15B.

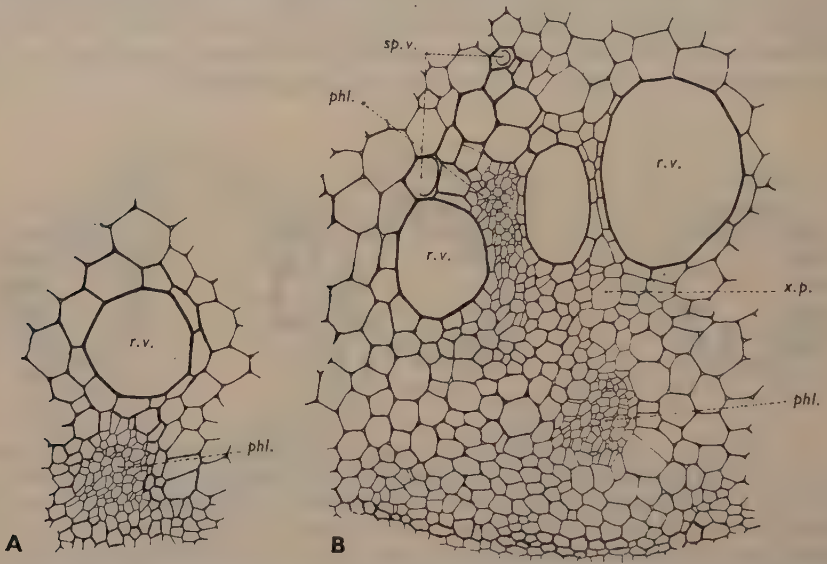


Fig. 15. Unusual vascular bundles. A. A cauline bundle that has been reduced to one-half. B. An abnormal union of a common and a dwindled cauline bundle, the common on the left and the cauline on the right. ×80. *sp.v.*, spiral vessels of the protoxylem; *phl.*, phloem; *x.p.*, xylem parenchyma; *r.v.*, reticulated vessels.

I would now indicate to the reader how the number of ridges, and of course the number of common bundles, alters from node to node. No two stems are alike; and two illustrations may be allowed to expose the way in which the number increases from the base to its maximum and then falls to the distal end:

First illustration, a stem with ridges rising to 18, but in general 16, basally 9 and distally 12, the internodes in order from base to distal end:

9 10 12 14 14 14 15 16 16 17 18 18 18 18 18 18 18 18 18
18 17 17 17 17 17 17 17 16 17 16 16 16 15 16 16 15 16 16
16 15 16 16 16 15 15 15 15 15 15 15 15 15 14 14 14 12

Second illustration, a stem that received the field no. 50 to which reference will again be made later. It had two ridgeless internodes underground, then the ridges from 13 increased to 16 and the stem in the end died exhausted with 8:

und. und. 13 13 13 12 13 13 13 13 12 13 14 14 15 14 15 14 15
16 16 15 16 15 15 16 16 15 16 16 16 15 16 16 16 16 16 16
16 16 16 16 16 16 16 16 16 16 16 16 16 15 15 16 16 16 16
15 14 15 14 14 14 13 14 13 12 13 12 12 11 11 11 12 12 12
11 10 9 8 9 8

In these stems, the changes are by one ridge at a time, but in other stems changes of two or three ridges at a time may be found near the base readily. This will be discussed later.

The maximum number of bundles is always at a little distance up the stem, and with the changes in number go changes in phyllotactic pattern.

13. The ganglion, a partial nodal plate

The term nodal plate will be familiar to most botanical readers as applied to the vascular nexus present so generally at a node; but there is nothing like a plate in *Tamus*, and what there is has the form of a ganglion. Falkenberg, who examined it in *Dioscorea villosa* Linn., called it an imperfect knot (*Vergleich. Untersuch. ü. d. Bau d. Vegetationsorg. d. Monocot.* (1876), p. 66).

The ganglion and the foliar emergence are parts of each other. Just after the initiation of the emergence the ganglion becomes visible in the subjacent tissue as a patch of eagerly staining meristematic provascular cells. The combination of emergence and ganglion makes what may be likened to a buoy afloat in the surface of the axis; the emergence is the part of the buoy in the air, the provascular tissue is the part of the buoy in the water. The latter, to complete the comparison, possesses five anchors as provascular strands which attach themselves down stem to slightly older provascular tissue, namely the nascent ganglia of older emergences; and it throws out at the same time three strands directed to the emergence, which are the initials of the leaf's three basal bundles; and these are continuous through the ganglion with the downward strands that become the common bundles. The other two anchoring strands become the cauline bundles.

I am aware that in recent years it has been stated that the vascular unions grow upwards, not downwards as was formerly believed; but it is difficult to regard this as so in *Tamus* where the position of their upper ends is certain and the position of their lower anchorage uncertain. If they do not extend in *Tamus* from the upper ganglion to the lower, they appear simultaneously in their whole length. Whether it be the one or the other, my argument is not weakened. The typical ganglion grows to the shape shown in Fig. 16, though of course not so clearly delimited. But the unusually large ganglion of scale-leaf *A* is of altered outline; and, as to the rest, their proportions in length and breadth are not always alike.

Though the number of vascular bundles that descend from a ganglion is unvarying, being the five that make up the leaf-trace, the ganglion does not control the number and nature of the bundles that anchor in it from above. They, in their anchoring, somewhat deform it. The bundles that descend from the ganglion are rather broad-based at their release: they rapidly diminish and then take nearly constant diameters. A consequence of this is that, for illustration, the bundles seen anchoring in the second component of Fig. 16 are smaller than the bundles seen issuing in the third component.

Ganglia have up-spiral and down-spiral sides as definitely as the leaf-traces (see p. 334), and an effect is seen in the third component where the inward terminations are somewhat unequal, or in the second component, where the anchoring bundles enter. The elliptic outline of the mid-common bundles in the second component arises in the obliquity of its section. The first and third components show that the common bundles do not lose their individuality in the ganglion; but the minute structure of the ganglion exhibits a passing over of elongated cells from one side to the other in an arch above the passing outwards of the mid-common bundle. From the ganglion at this point arise the bundles to the axillary bud or buds.

The ganglion is a more important structure than the vascular bundles, coming in time before them; and it has the appearance of playing a part in their initiation.

The part of a petiole between its two pulvini contains more than three bundles, but does not receive from the ganglion more than three; the extra bundles arising in the petiole as branches. Still more extensively does branching characterize the bundles in the lamina. But there is never branching of bundles in the stem. Sinnott (in *Amer. J. Bot.* (1914), 1, 305) argued reasonably that to have three bundles passing to the leaf is primitive in the dicotyledons; and I would comment that we may add to the several dicotyledonous characters seen in the Dioscoreaceae this of having three bundles entering foliar organs. Scale-leaf *A*, already pointed out, is exceptional in having more than three.

The second component of Fig. 16 shows the anchoring, or perhaps it were better to say interception, of three common and two cauline bundles by the ganglion, and that they are not in the order that they have in a leaf-trace, common outside and medial, cauline pectinated between the common. Change being frequent and the common bundles being under the ridges, ridge cannot regularly and exactly succeed ridge in the passing from one internode to another; but there is a trivial and unnoticeable adjustment about the margins of an axil.

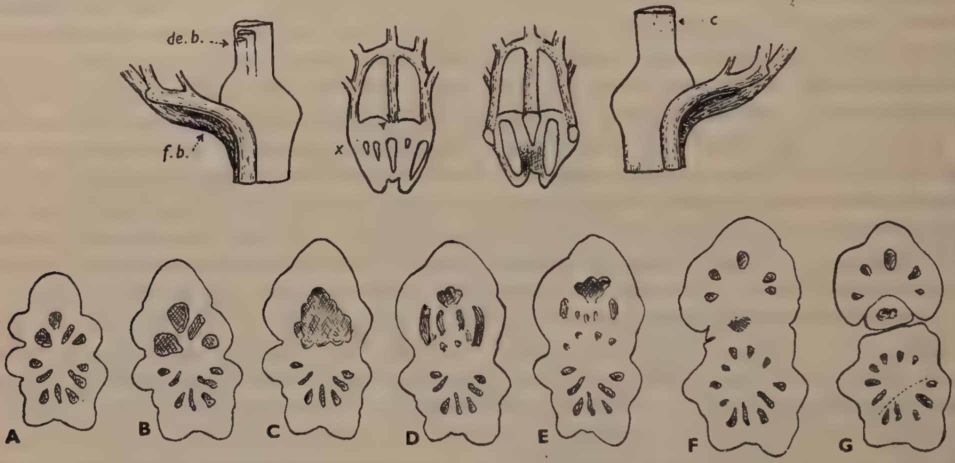


Fig. 16. (Above), a nodal ganglion seen from either side, from above and from below: *de.b.*, bundles that descend to it; *f.b.*, bundles running out to the emergence; *x*, bundles to the axillary bud; *c.*, a cauline bundle descending and by its size and position preventing the others from being seen. (Below), a series of sections through a node in the more slender distal part of the stem, showing that the ganglion may be carried outwards into a pediment. In component **G**, a dotted line indicates which bundles compose the leaf-trace of the next leaf.

The ganglion of Fig. 16 is commonplace in that it takes and gives the same number of bundles. Where the number of the ridges is altered upwards or downwards, the number taken is either above or below five. Not only do those enter the ganglion which would seem by position unable to pass it by but, as will be shown later, bundles in a position to make near misses may be deflected to a ganglion.

The ganglion is thus the place where all alterations in bundle arrangements are made; it is a body astride channels by which many activities are furthered. Whether it can originate growth-stimulation or cannot, substances that have their place in stimulation must pass through it.

14. THE INCONSTANCY OF THE DIVERGENCE OF THE LEAVES

The inconstancy of the number of ridges on an internode, the ridges being related to bundles in the leaf-traces, declares that the leaf-divergence must be inconstant. It is considerably so. But that which is inconstant need not be in disorder; and our immediate inquiry is to seek order. It has long been recognized that divergence is less constant in the monocotyledons than in the dicotyledons. Hofmeister's statement on p. 461 of vol. I of his *Allgemeine Morphologie* (1868) refers to inconstancy in *Luzula* and some other plants of the monocotyledons. The divergence can change too rapidly in that genus for convenient study: *Tamus* offers itself more conveniently, as the change is less rapid; but unfortunately the labour of measuring successive divergences is so slow in its rewards as to forbid the desirable statistical treatment. In default I am driven to take illustrations from individual plants. I have selected four, the stems of which were examined in detail, internode by internode, from end to end, the divergences being worked out by the use of the ridges and their underlying common bundles. The four stems provided 226 determined divergences, ranging from 45 to 292°. Uninformed observers might say that the direction of the genetic spiral had been reversed in such divergences as were above 180°: that would be erroneous; and the genetic spiral is of constant direction. The divergences above 180° *are* abnormal from another cause; and so I class them in the following statement. The divergence of 45° is also abnormal.

	Cases
Abnormal divergence below 80°	1
Subnormal, between 80 and 120°	36
Normal, from 120 to 140°	117
Supranormal, above 140 and up to 180°	55
Abnormal divergences above 180°	17

For the moment let the interest rest on the range of the divergence, and let the classification of the marginal cases as abnormal be justified when the data have been fully exposed in Table 3. Is the variability about a single mode? Apparently, the mode being in the neighbourhood of 130° if the abnormal cases be excluded; and 130° is truly in the middle of what are called normal in the statement above. The following figures of averages of the sums of the divergences of all the internodes with 13, 14, 15, 16 and 17 ridges may be adduced as indicative of 130° being near the mode:

Number of ridges ...	13	14	15	16	17
Available observations ...	18	31	47	67	12
Average divergence (°) ...	134	131	130	131	125

A phyllotactic pattern with constant divergence of 130° is, however, absolutely impossible in *Tamus*, the fraction being 13/36; for that, the thirty-seventh leaf should stand above the first; and the pattern demands an unattainable number of ridges. A mode is but theoretical; and there certainly is no one divergence that in *Tamus* is optimal for the purpose of securing as much assimilation as possible, otherwise why the mobility of the petioles by which great rearrangements of the laminae are contrived?

Divergences originate in the very apex of the axis out of the rhythm in which morphogenetic fields for giving rise to foliar emergences are produced. These fields become self-centred and so become isolated. Thereafter the retention of the divergences, as originated, depends on the uniformity of the subsequent expansion; but the expansion need not be uniform. For instance, in some plants such as *Equisetum* extraordinary displacements follow the rhythmic cutting off of sectors from the apical cell. But expansion that is not uniform is not to be assumed probable; for growth usually maintains the phyllotactic pattern originated at the very apex. When we diagrammatize this pattern on paper it is symmetrical about its centre, and the stichies—blastostichies if through the emergences—which can be superposed on the diagram, curve alike and are evenly disposed; moreover, so long as the fields have been given off one at a time, it is possible to superpose a spiral line, the genetic spiral, which passes in turn through each emergence in order of age. So drawn, the genetic spiral is an abstract descriptive conception; but in a study of the apex we find it to have one concrete property, namely that the plant determines at the very apex the direction in which the spiral shall turn. It has seemed to me that various writers have confused the abstract and concrete to their own disadvantage; and some have relied in argument on 'contact stichies' for stichies midway between blastostichies at a phase in growth when contact is no actuality.

There is a possibility of the apical rhythm changing: if it changes, it is natural to expect that the change comes gradually. It certainly changes in the apex of *Tamus* and brings changes into the phyllotactic pattern. An examination into the rhythm must start with an examination of the patterns. There is a difficulty here: it is difficult to decide how much repetition leads to a pattern in phyllotaxy; and I have decided to use the word 'pattern' for incipient as well as established pattern. The reader thus forewarned will not be misled, and I shall proceed to demonstrate some patterns.

Fig. 17 includes a camera-lucida drawing of one section out of a series through an apical bud taken from the ground in the month of February, at which time enough

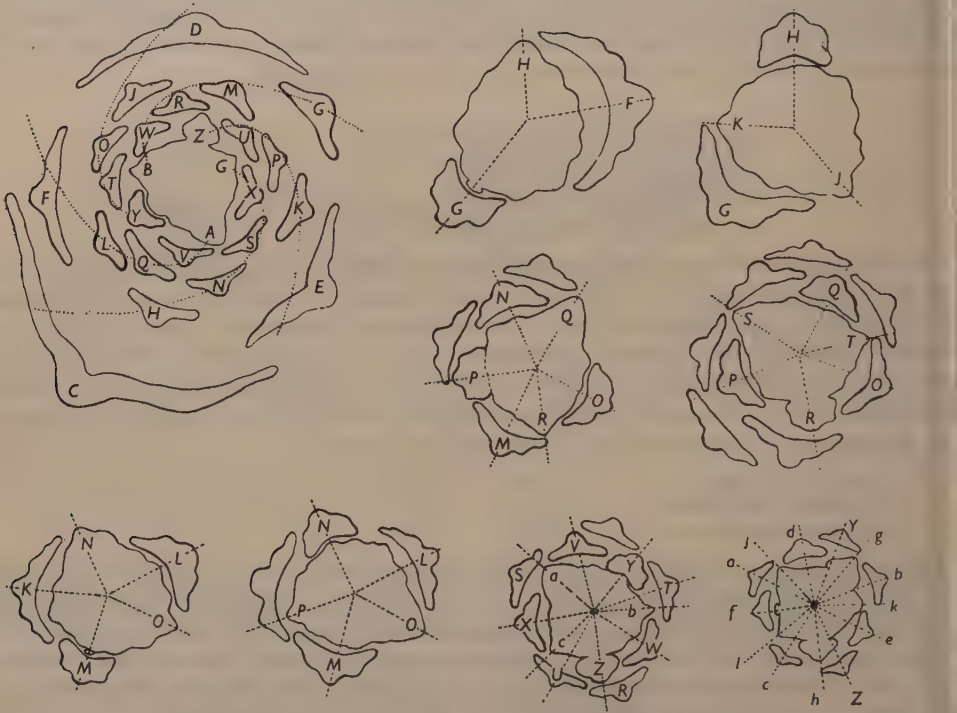


Fig. 17. Camera-lucida drawings from a series of sections through an underground bud taken in February. The first gives the positions of all the emergences from *C* to *Z*, the last being at the horizon of this particular section. Five short-way blastostichies are inserted; they and the orthostichies point to the pattern being 5/13: the other drawings are at the several horizons their letters indicate, the horizons having been chosen because no displacement of the emergences examined could have taken place. The results are explained in the text.

stem had been produced to throw scale-leaves *A* and *B* out of the picture, so that the drawing does not show them: but it shows the relative positions of all the emergences from *C* to *Z*, twenty-three in number.

Short-way blastostichies have been dotted into the drawing and are five in number. They have been geometrically drawn and they pick up the successive emergences satisfactorily for a bud which, by being rather loose, allows the distal ends of the organs latitude of displacement. Inspection of the drawing shows *H* to be more or less outside *V*, and *J* to be more or less outside *W*, the emergences being the thirteenth from each other. The phyllotactic pattern is, therefore, by this evidence 5/13 or 138·46° of the circle.

The rest of the drawings in Fig. 17 are checks to this conclusion. Where *G* had just been freed and *H* had not, *G* and *H* therefore being tied to each other, the divergence was read as 140°. In the next section, where *H* had just been freed and *J* had not, the divergence of *J* from *H* was read as the same. And in this way readings were carried through all the drawings; this is what they gave in series beginning with the relation of *F* to *G*:

140 140 140 135 145 140 140 140 145 130 142 134 135 140
140 140 140 140 135 140 135 140 138 130 145 138 135 140
Average 138°.

I admit that angles thus measured cannot have absolute accuracy (cf. Schoute in *Rec. Trav. bot. neerland.* (1925), **22**, 139), but used as averages in cases where the axis is almost circular, I claim them useful; and I call attention to the circumstance that the average was exactly that suggested by inspection.

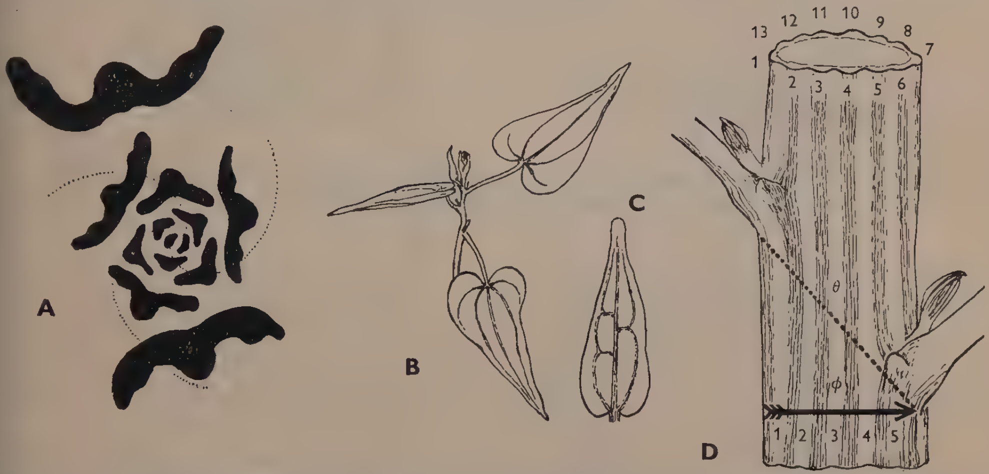


Fig. 18. **A.** A camera-lucida drawing of a section selected out of a series cut through the dying bud of an exhausted stem, the month September. The blastostichies are three in number and the phyllotactic pattern more or less 3/8. **B.** The end of an exhausted stem showing the abrupt arrest to the growing of the leaves; × ½. **C.** The first of the arrested leaves showing the stage at which arrest was done; × 10. **D.** A short length of a stem, covering two nodes, the stem with thirteen ridges. The arrow near the base overlies the five ridges of the divergence of the upper leaf from the lower. Thus it is 5/13. True divergence along the line θ cannot be measured owing to the growth in length of the stem and what is called divergence, angle ϕ, is our best makeshift.

Before passing on, it may be added that other buds of the same age and same stage of development have shown the same phyllotactic pattern. It is displaced upwards, as I shall show.

Fig 18A is a drawing from a series of transverse sections through the bud of an exhausted stem dying in September. Its obvious blastostichies are three and run counter to those of Fig. 17; and the whole pattern is most obviously not that of Fig. 17. It is just another that is possible of development. But a determination of its angles by inspection cannot be confirmed as were those of Fig. 17 because the axis was far too irregular for the determination of its centre; in fact some of the pediments were almost as large as the axis proper.

Two botanists have published, in diagrams of the course of the vascular bundles, a phyllotactic pattern which each thought to be that of *Tamus*. Neither appreciated the fact that the pattern is inconstant and neither shows that he had extended his examination far enough to justify his pattern. Queva (in *Mém. Soc. Sci. Lille* (1894), sér. 4, **20**, pl. 5, fig. 1), composed a diagram extended over six nodes, each node holding thirteen common and ten cauline bundles. The divergence of his plan works out at 141°. I suspect that having found one or perhaps two internodes pointing to this, he extended it in the belief that it was constant. Bucherer (in *Bibl. bot., Stuttgart*, Heft 16, pl. 4, fig. 3) gave a diagram which he extended over seventeen internodes, with sixteen common and eight cauline bundles arranged in a way which to me is incredible even as an accident. I propose to take the reader to the plant afresh in an examination of four selected stems from end to end; and as a preliminary I refer him to Fig. 18D which represents a short internode

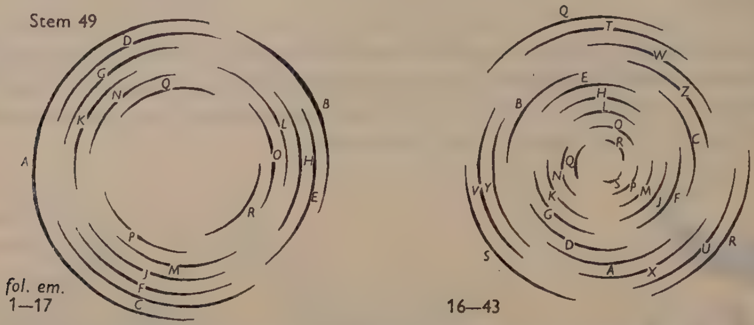


Fig. 19. Phyllotactic arrangement of all the forty-three foliar emergences (*fol. em.*) along stem no. 49 worked out by employing the ridges.

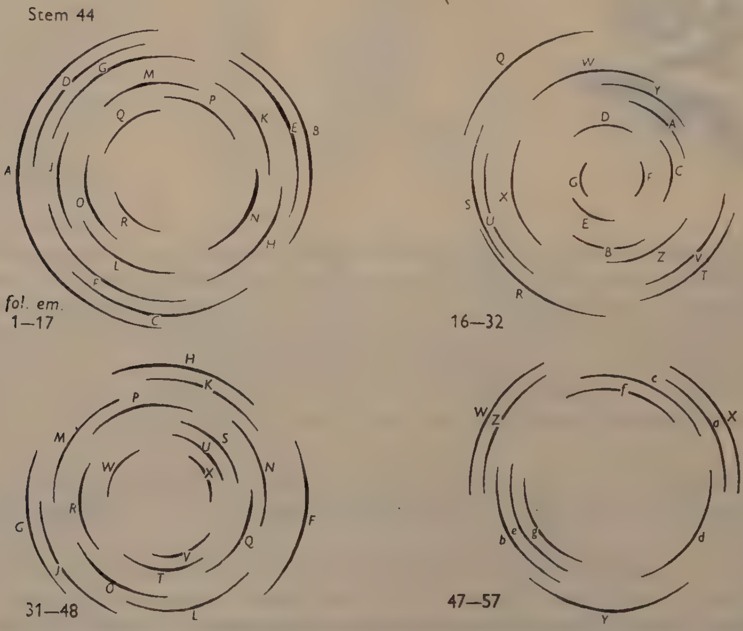


Fig. 20. The phyllotactic arrangement of all the fifty-seven foliar emergences along stem no. 44 worked out by employing the ridges.

with thirteen ridges. Between the ridge over the mid-common bundle of the lower leaf and the ridge over the mid-common of the upper are four ridges, so that the central point of an axil is five ridges from the next and the phyllotactic pattern is 5/13. The arrow ϕ covers the five; that is, it covers the sector which botanists take for use in phyllotaxy because the real divergence θ cannot be used. Along the four selected stems, angle ϕ was measured in units of bundles and the results were recorded in diagrams. In such work, if internodes be long and contorted on themselves, it is at times helpful to inject bundles with a colouring fluid. The stems were taken as late in the season as possible so that no further growth could take place. One of them was that of a plant apparently in its first year of flowering, a female plant from the north-east face of a sharply defined belt of trees where the light appeared to be equally dispersed up to the height that the plant reached.

As I was seeking the stem of a plant just mature and recognized indications of this being such in its symmetrical tuber with an absence of subsidiary heads, it was taken and received the field number 49. Another plant to which the number 50 was given, was taken as a contrast, having a very vigorous stem from a large irregular several-headed tuber. Two other stems, one male and the other female, were taken as intermediates. I do not give the data gathered, but give more informative diagrams made from them, with lettering on them that shows accurately the sequence of the emergences and their radial position. The simplest stem is the first (Fig. 19); the longest is the last (Fig. 22). Tristichy began in the simplest at *B*, and continued to the end, but passed from a condition almost ortho-tristichy to marked spiro-tristichy. In contrast, tristichy was never obvious in the longest stem, no. 50 (p. 344).

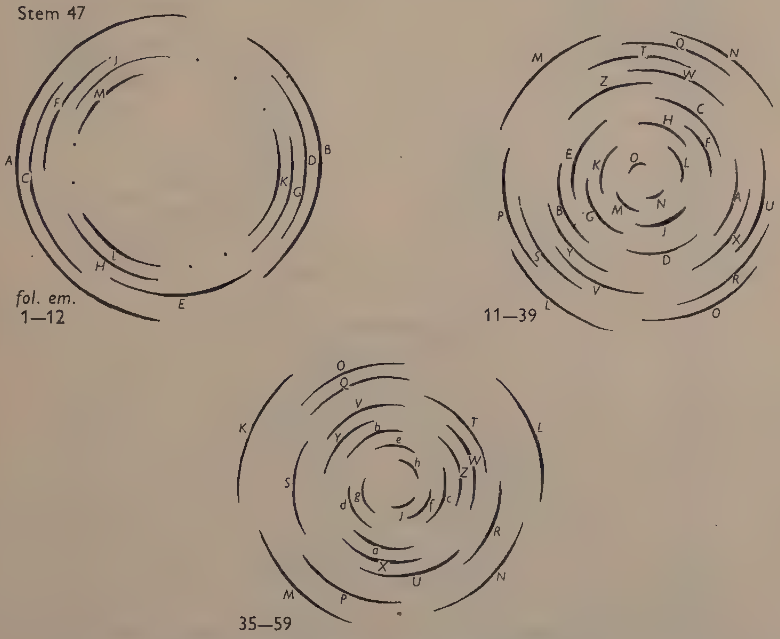


Fig. 21. The phyllotactic arrangement of all the fifty-nine foliar emergences along stem no. 47 worked out by employing the ridges.

Stem no. 44 was the next in vigour after no. 49, being that of a fully mature plant of somewhat greater age than no. 49. Its leaf-arrangement was much less regular; in fact it might be called irregular, as I shall have cause to explain in describing Fig. 24. The other two stems, likewise judged of older plants than no. 49, also showed irregularities as if irregularity is connected with that greater size of stem which comes with greater age. To enable the nature of the irregularities to be laid bare, I gather into Table 3 a statement of all the angles observed (these are the figures in brackets), along with the number of occurrences (these are the figures after the brackets); the columns represent the number of ridges from one leaf to the next and the rows the number of ridges about the whole stem. The table is to be read thus: of internodes with eight ridges two had a divergence of 180°; of internodes with nine ridges one had a divergence of 120°, three of 160° and one of 200°; and so on. In this way the table shows what divergences were most prevalent,

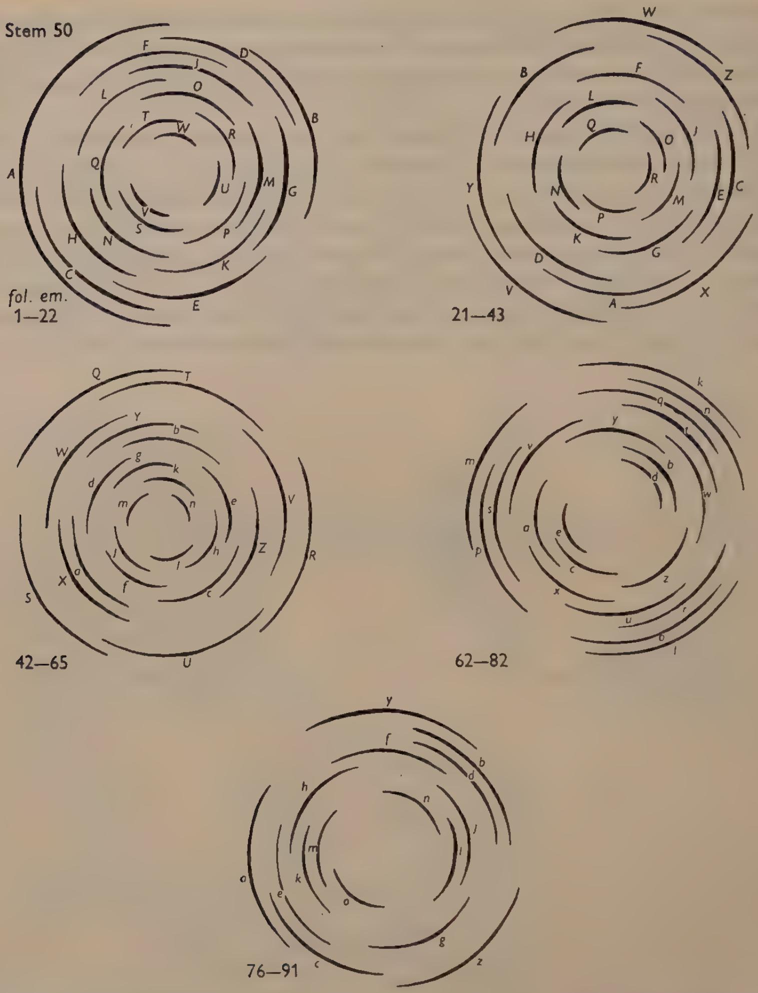


Fig. 22. The phyllotactic arrangement of all the ninety-one foliar emergences along stem no. 50, worked out by employing the ridges.

TABLE 3. *The frequency of different divergences on the stems* 49, 44, 47 and 50; *degrees of divergence in brackets*

No. of ridges on the stem	No. of ridges indicative of divergence											
	2	3	4	5	6	7	8	9	10	11	12	13
8	—	—	(180) 2	—	—	—	—	—	—	—	—	—
9	—	(120) 1	(160) 3	(200) 1	—	—	—	—	—	—	—	—
10	—	(108) 1	—	(180) 1	—	—	—	—	—	—	—	—
11	—	—	(131) 3	(163) 1	(169) 2	—	—	—	—	—	—	—
12	—	—	(120) 1	(150) 7	(180) 2	—	—	—	—	—	—	—
13	—	—	(111) 5	(138) 11	(166) 2	—	—	—	—	—	—	—
14	—	—	—	(129) 27	(154) 2	(180) 2	—	—	—	—	—	—
15	—	—	(96) 5	(120) 22	(144) 15	(168) 5	(216) 2	(240) 1	(264) 2	—	—	—
16	(45) 1	—	(90) 4	(112) 12	(135) 44	(157) 5	(180) 2	(202) 1	(225) 3	(247) 2	(270) 1	(292)
17	—	—	—	(106) 5	(127) 3	(148) 4	—	—	—	—	—	—
18	—	—	(80) 1	(100) 3	(120) 5	—	—	—	—	—	—	—
Total	1	2	24	90	75	16	4	2	5	2	1	1

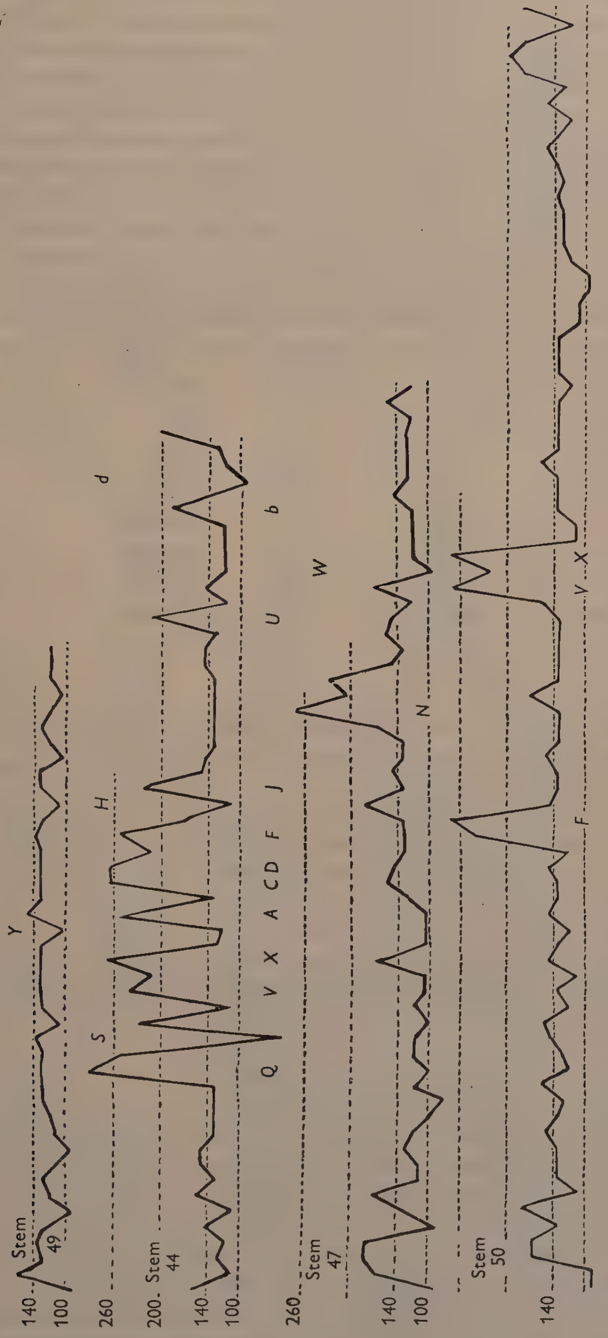


Fig. 23. Graphs showing the successive divergences along stems 49, 44, 47 and 50; the higher the line the greater the divergence. The letters are those of the upper foliar emergence of each unusual divergence, and indicate their positions.

e.g. 135° associated with sixteen ridges, 129° associated with fourteen ridges and 120° associated with fifteen ridges. The summing at the base shows the most frequent number of ridges from one leaf to another to be five or six, so that a curve of error would have its mode between five and six, but it would be skew by an extension to the right, caused by divergences higher than 180°. Of each of these higher divergences there were few, and with the aid of Fig. 23 it can be made evident that they are doubled divergences arising from suppressions of foliar emergences. As the reader will understand they are the abnormal divergences of the lowest line of the statement on p. 339; and are divergences which the graphs of Fig. 23 show absent in the stem only just mature, crowded into the central part of stem no. 44 and sporadic in the other two. Three considerations demonstrate their doubled origin: (i) in the bottom line of Table 3 they are dysgenic to the Galton curve which the rest make; (ii) the presumed missing emergences, if restored to places in a phyllotactic diagram, in a general way complete it; and (iii) complete suppression can be demonstrated to be of possible occurrence. As evidence for (i) it suffices to tabulate, as follows, the presumed doubles in column against those which are not doubled:

	Degrees	Cases	Degrees	Cases
Abnormal	Less than 80	1	—	—
Subnormal	80–89	1	—	—
	90–99	9	—	—
	100–109	9	200–218	4
	110–119	17	220–238	3
Normal	120–130	59	240–258	3
	131–140	58	260–278	3
Supranormal	141–150	26	280–298	1
	151–160	10	—	—
	161–170	10	—	—
	171–180	9	—	—

As evidence for (ii), Fig. 24 has been prepared. It gives the positions of presumably suppressed emergences in the very irregular part of stem no. 44 and may be left to tell its own story.

To obtain evidence for (iii) an experiment was performed: a vigorous axis was decapitated so that the senior bud in the axil below the decapitation was strengthened for growth. When that bud had grown out and its stem had become stout, it also was decapitated, so that the second bud was released for growth, the purpose being to create inadequate room for the third bud. Then the axil was taken, preserved and sectioned in series. Fig. 25 contains outlines of every other section of the pertinent part of the series. The numbers of the sections are set against them. The position of the mid-rib of the axillant scale-leaf indicates displacement. The first emergence of the bud is lettered *A*, the second *B*, and so forward. In the first component *A* and *B* are almost freed. Some 30μ higher, in the second component, *A* is seen to have been freed. This organ if traced through the series is found to have outgrown and overtopped the bud, being about 400μ long. *B* became free immediately afterwards, grew larger than *A* and overtopped the bud by more than *A*. *C* was emergent in the third component but not freed, remaining as no more than a ridge, almost but not quite suppressed! *D*, escaping suppression, was freed at the horizon of the eighth component and had a limb almost 50μ long. The next emergence appeared close to *D* and on the wrong side of it, i.e. it had a divergence larger than 180° because, as I understand it, *E* proper had been completely

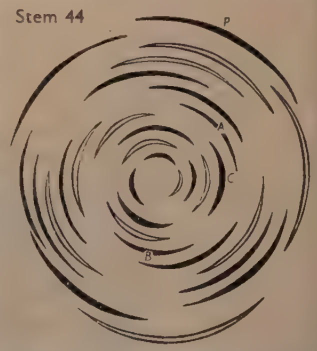


Fig. 24. The phyllotactic arrangement of the emergences in the most irregular part of the stem no. 44 with the presumed suppressions inserted. The latter are outlined only, the others black.

suppressed and that which followed had become *E*; E_2 we may call it. *F* appeared in the tenth component and was freed. *G* suffered as *C* had done, developing to the condition of a ridge and did not become freed. *H* and *J* were both freed. The reader will observe that the emergences *C*, *E* proper and *G* had positions where interference arising from the proximity of the second bud would, if anywhere, be most expected. We are not entitled to postulate the exact nature of the interference. But that suppression occurs sometimes so early that no trace is left, is evident; and the evidence leads to thinking maladjustment in phyllotaxy a contributing cause in the irregularity of stem no. 44. I have sometimes found on internodes small wens which seemed to be indications of suppressed emergences; and I have without method examined short lengths of many stems finding in them wide-angled divergences so often that, on the evidence of divergence, suppression in *Tamus* is by no means uncommon.

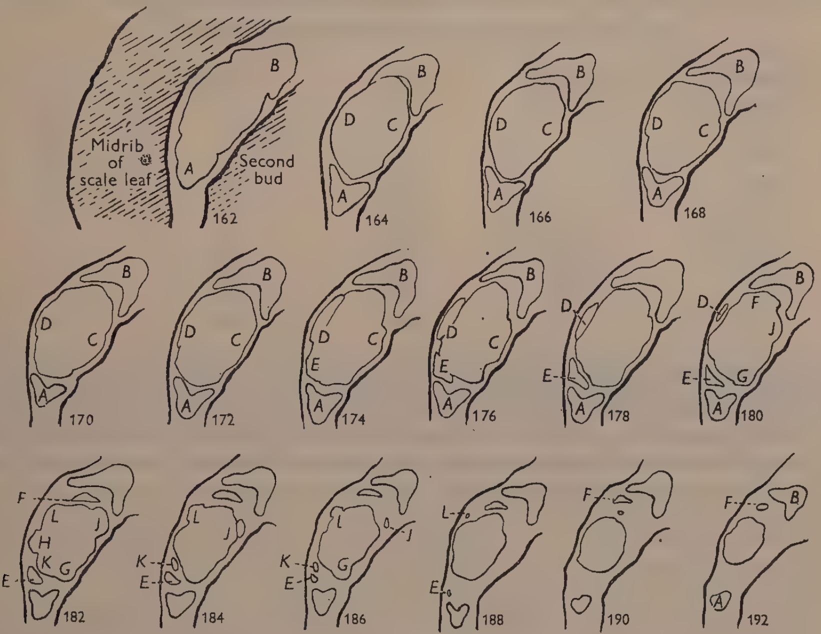


Fig. 25. Camera-lucida outlines of sections about 30μ apart through the third bud of a crowded axil. The first drawn shows the margin of the second bud and the position of the axillant leaf between which the third bud was compressed enough to be out of the mid-line. Letters indicate the successive emergences of the bud.

Obviously if the wide divergences of Table 3 are doubled, the very narrow divergence in stem no. 44 (Fig. 20) is the complete splitting of a single component. I have figured incomplete splitting (*Proc. Linn. Soc.* (1943), Sess. 155, p. 33).

Suppressions may occur in any part of a stem, but congregate where it is of greatest diameter, so that if the divergence angles be summed in tens and the averages extracted, as in Table 4, stems 44, 47 and 50 show maxima in the third, fourth and fifth decades respectively, and stems 47 and 50 show a higher average at the base than just above it. But if the table be rearranged with each angle above 180° taken as two emergences, Table 5 results and the higher averages marked by bold type in Table 4 are eliminated. This elimination goes a long way towards demonstrating that the wide divergences are doubled. But the relatively high averages in the lowest or lower two decades have a different cause which will be exposed in the discussion of stem no. 50. Stem no. 50 (Fig. 26) started its emergence formation with a spiro-distichy strongly antidromous to the genetic spiral and therefore indicative of an angle of divergence well below 180°.

TABLE 4. *Average size of divergence angles in decades along stems* 49, 44, 47 *and* 50

No. of internodes	Stem 49	Stem 44	Stem 47	Stem 50
81–90	—	—	—	161
71–80	—	—	—	132
61–70	—	—	—	123
51–60	—	144	129	136
41–50	120	140	131	**160**
31–40	119	158	**173**	154
21–30	129	**211**	129	131
11–20	126	162	119	147
1–10	120	122	135	142

TABLE 5. *Average size of divergence angles in decades along stems* 49, 44, 47 *and* 50, *angles of over* 180° *regarded as double*

No. of internodes	Stem 49	Stem 44	Stem 47	Stem 50
91–100	—	—	—	143
81–90	—	—	—	126
71–80	—	—	—	133
61–70	—	125	135	124
51–60	—	130	125	132
41–50	120	135	128	133
31–40	119	126	140	140
21–30	129	123	129	131
11–20	126	137	119	147
1–10	120	122	135	142

The two blastostichies of this distichy run through *A–C–E* and *B–D–F*. Then the distichy was displaced by pentastichy, with blastostichies as the figure explains. Two of the stichies of this pentastichy fit those of the distichy and make logarithmic spirals when plotted; the three new stichies show some irregularity. That all three appear so nearly on one horizon is interesting because the change is less gradual than might have been expected. At the centre of the first component of this figure are the emergences *Z* and *A* (second series) which do not fall into the pentastichy; the second component shows that they fall into a tristichy which for a short distance displaced the pentastichy, only to be displaced by a return to pentastichy. The reader will see this tristichy in *V–Y–B*, *W–Z–C* and *U–X–A–D*. He will note that beyond *B* is evidence of a suppression and also beyond *D* and that unexpectedly close to *C* is *E*; and I suggest that the two suppressions have been induced by the misfitting of the phyllotactic patterns at the transition. The two belts of pentastichy belong to the 5/13 pattern; the intervening tristichy to the 3/8 pattern. After the second belt of pentastichy and some confusion tristichy returned

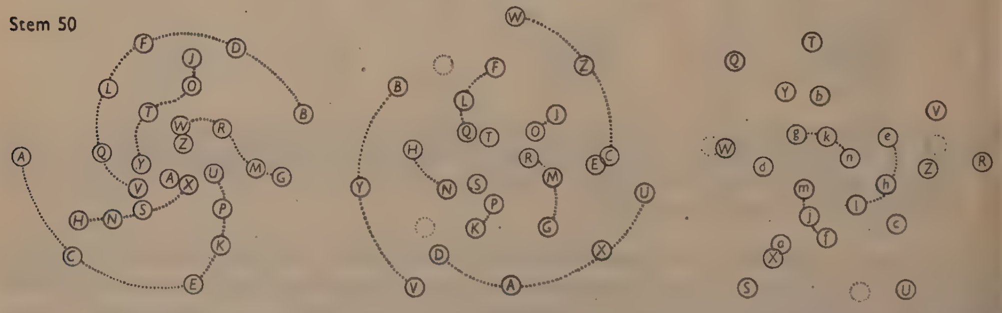


Fig. 26. A diagram indicating the apparent blastostichies and probable suppressions (dotted circles) over the first two-thirds of stem no. 50. Explanation in the text.

and continued to the end of the sequence. There were enough emergences beyond the last of the third component to fill a fourth component; as they showed tristichy without irregularities to give them an interest, I omit this component. In the confusion of the third component there were some suppressions.

The initial distichy was probably laid down in the calyptrate bud before or immediately after it was released to grow at the end of the summer; the first pentastichy was probably laid down in autumn and early winter; the first tristichy and succeeding pentastichy perhaps in late winter and the tristichy that followed might have been commenced in very early spring, all, it must be noted, during complete reliance on the tuber for food and before seasonal warmer conditions could influence the phases. The suppressions appeared when food supply was regular; and, moreover, appeared as if by misfits consequent on changes in the pattern, not by prohibition of the formation of morphogenetic fields, but by interference with their development.

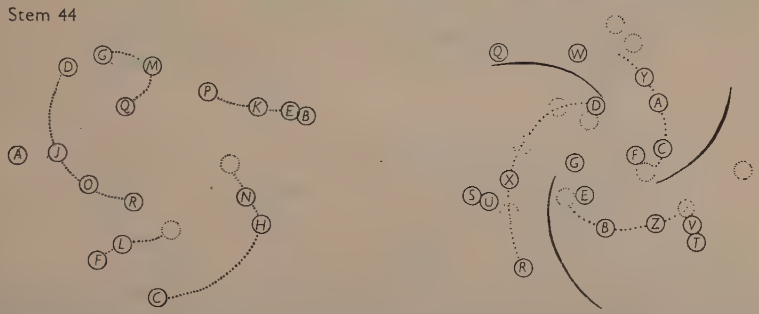


Fig. 27. Diagrams suggesting the blastostichies of the first half of stem no. 44 and the presumed suppressions (dotted circles). In the first component pentastichy displaces distichy and ends with suppression. The confusion is great in the second component and the diagram begins with the twinning of *R* and *S*; but it is very probable that the tristichy suggested underlies the confusion, and it is easy to make three groups of emergences as defined by the continuous lines.

Stem no. 47, examined in the same way as stem 50, had at its very base the distichy that is invariable at that horizon; then an approach to ortho-tristichy which, distichy not being altogether overcome and returning, by the combination with tristichy gave that pentastichy of two turns of the spiral that is so familiar; then disorder out of which tristichy was definitely established. There were suppressions both where the initial distichy gave way and in the subsequent disorder.

Stem no. 44, after its initial distichy, entered on pentastichy which was followed by confused tristichy. I give in Fig. 27 diagrams of the first part of this stem; as the first component suggests, the pentastichy ended with two suppressions. Also it shows *G* displaced. The pentastichy passed away in the confusion of the second component. Tristichy underlaid it to a sufficient extent that the emergences fell into three groups, and the pattern appeared to be 3/8. As already suggested *R* and *S* arose by the splitting of one field. In the central part of this decidedly irregular stem doubled divergences were as many as 10. A glance at Fig. 23 shows how thickly they were strewn.

This section has demonstrated how variable is the phyllotactic pattern and has put forward as one consequence of this, suppressions of emergences. It has shown that in a diagram order begins to appear through the disorder when the places of the suppressed emergences are filled; and that certain patterns may be expected in certain horizons of the stem.

15. Circumference and the number of bundles

This section shows the relationship of the circumference to the number of bundles present. The work for it was done in the autumn a year after the work of the preceding section, as late in the season as possible that all growth might have ceased. The exacting nature of part of the work caused me to limit to five the stems studied, and unfortunately the examination of the fifth and largest could not be completed as sloughing of the cortex began to interfere with the measuring. The four stems that were examined in full supplied the graphs in Figs. 28–31. A few notes must suffice regarding the fifth; and they will be inserted later.

The examination of the stems was conducted in the following manner: transverse sections were cut at mid-length of every internode and were drawn in outline under a camera-lucida at a magnification of twenty-eight diameters and the nature and positions of all the bundles present were inserted. After this preparation the diameter of each internode was ascertained by as many measurements as necessary and the circumference was calculated from the diameter. A count of the common and the cauline bundles followed, and the graphs here published were prepared. That of the shortest stem is given first place and so to the longest.

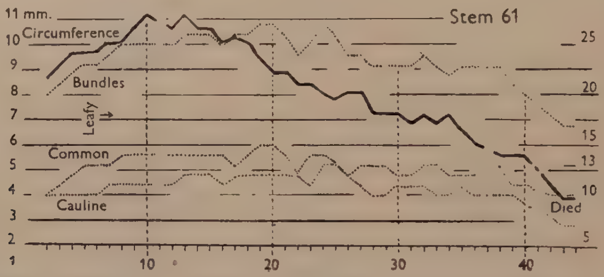


Fig. 28. Graph comparing internode by internode the circumference of stem no. 61, with the number of bundles present. The circumference is in millimetres by the scale on the left, the bundles by number by the scale on the right. There are three curves for the bundles, the total number, the number of common and the number of cauline. The stem carried assimilating leaves from the point indicated and had died at the tip. The internodes are numbered below. Where the curves are broken there was no measurable internode between two closely approximated leaves.

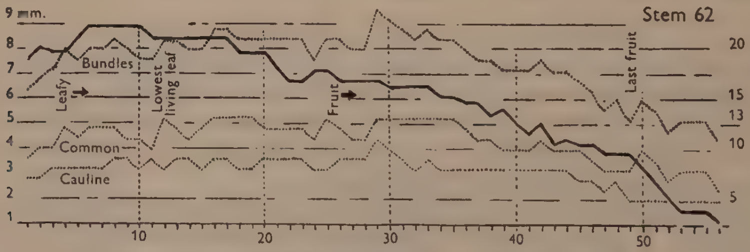


Fig. 29. Graph of stem no. 62 on the plan of Fig. 28.

In all four graphs the thick line relates to the circumference of the internodes at mid-length according to the ordinates on the left; the dotted lines give the number of bundles present according to the ordinates on the right. There are three dotted lines, one for the common bundles, one for the cauline bundles and one for the sum of the two. The ordinates have been so adjusted as to bring the curves of circumference and total bundles into apposition, so as to make it easy to see that though the upper curves do not follow the very same track there is considerable agreement. In bringing the curves into apposition the ratio of 2½ bundles to 1 mm. of circumference was adopted. As the tracks diverge, the average width of a ridge is no constant fraction of the circumference, for if it were they would not diverge; but at the same time the average width is manifestly in relation to the circumference, for were there no relationship no measure of agreement would be present.

On p. 326 I showed that pediments descending from foliar organs increase the diameter of the internode but do so less and less the further from the upper leaf; but if internodes are very short there may still be an effect on the diameter at mid-lengths due to the pediment. On that account I have marked the position of very short internodes by asterisks, in order to admit that irregularity of the thick line where the asterisks are may arise in this way. Where the lines are broken the internode was absent, with the consequence that two leaves stood side by side, but not opposite (there never are any opposite leaves in *Tamus*). The abscissae numbered along the bases of the figures indicate the internodes by number: there were forty-four of them in the shortest stem and 102 in the longest.

The shortest stem (field no. 61) came from a hedgerow over the face of which it had climbed and along the top of which it had spread a little; its tip had died, and it had not flowered. At the base it was just over 9 mm. in circumference and at its maximum diameter, the 10th internode, just over 11 mm. The 11th internode had been suppressed bringing leaves *K* and *L* to the same horizon, the only suppression of an internode in this stem. From the horizon of the 12th internode the circumference diminished to the distal end. The maximum number of bundles had not been attained at the maximum circumference, but was attained a few internodes higher; and after it had been attained the number fell to the distal end.

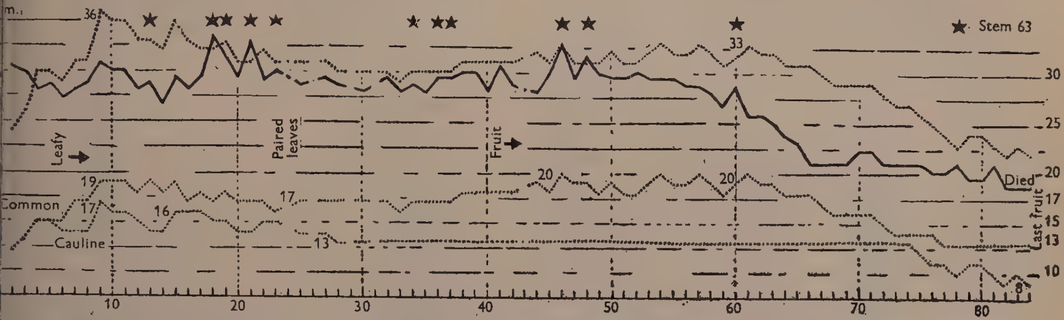


Fig. 30. Graph of stem no. 63 on the plan of Fig. 28. The asterisks along the top indicate very short internodes in which the descent of the pediment to beyond mid-length raised the diameter.

The stem next to this in length (stem no. 62 and Fig. 29) increased in circumference to the 6th internode, kept its maximum to the 10th and then diminished to the distal end. It was female and carried fruits from the node between internodes 25 and 26. As in stem no. 61, the maximum number of bundles was later than the maximum circumference and indeed a little beyond the horizon at which fruits commenced. No internodes in it were completely suppressed.

The third stem (field no. 63 and Fig. 30) was of another fruiting plant. Its tip had died back to the 85th internode but there was fruit up to the node immediately before (one berry only at this node). The maximum circumference was in its 18th internode; and from this the stem remained relatively stout to the 46th whereafter it diminished to the distal end.

The fourth stem (field no. 64 and Fig. 31) was male and had flowered from the node between the 10th and 11th internodes, continuing to flower at every node thence to the extreme end. The reader will observe that the curve of diameter begins high and descends through two internodes consequent on the thickness of the cortex as they were underground. The interest of the curve begins after them. The stem reached its maximum circumference in the 22nd internode whence the circumference fell to the distal end; but it was very uneven, very largely from the obvious cause that there were many short internodes intermingled with not a few cases of suppression of internodes. One would expect the one to accompany the other.

The better to appreciate the relationship of circumference to the number of bundles, all the curves were smoothed by moving averages and thus smoothed collected together into Fig. 32, wherein curves of number of bundles are placed as nearly over the others as their unevennesses permit.

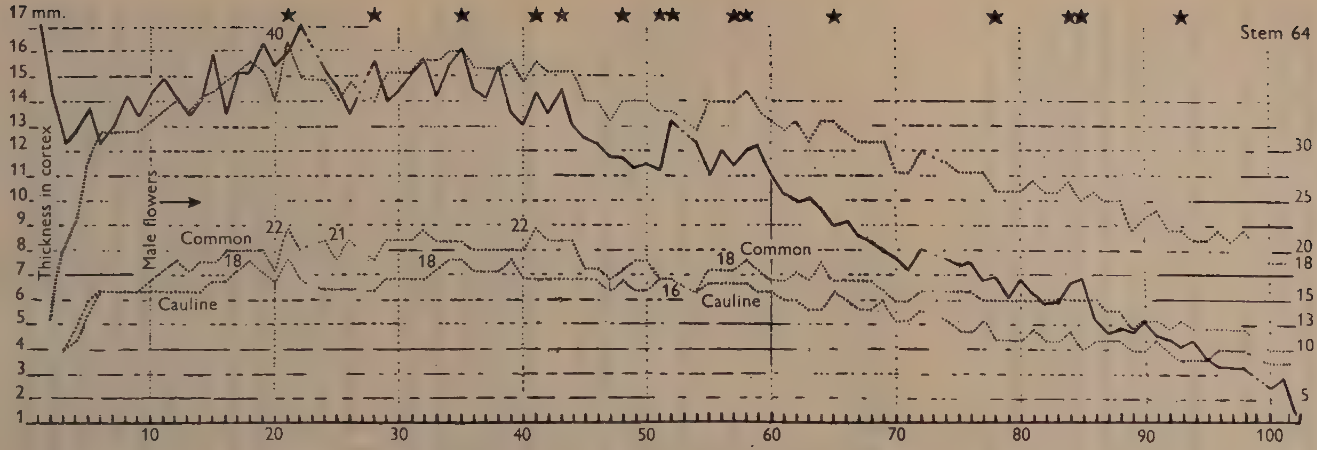


Fig. 31. Graph of stem no. 64 on the plan of Figs. 28 and 30.

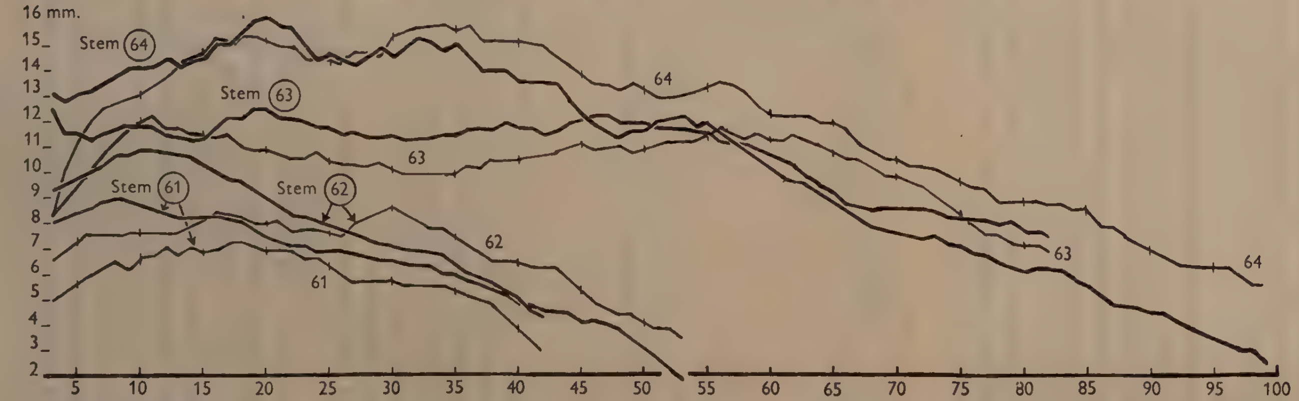


Fig. 32. Graph giving the curves of the circumferences of all the four stems, nos. 61–64, after smoothing by a moving average; ordinates indicated on the left, enumeration of the internodes below; and over the curves of circumference, the curves of number of bundles have been drawn so as to indicate the greatest correspondence. The latter are marked by a cross bar at every fifth.

The moving average makes the increases to the maximum and subsequent decreases extremely obvious and understandable in regard to the rather regular shorter stems nos. 61 and 62. It is less so in the longer stems as they lack regularity. This induces me to recall that stem no. 49 was said on p. 343 to possess simplicity and regarded as only just at maturity. Obvious also is the fact that there are fewer bundles to a unit of circumference in the internodes at the base of the stem than in the internodes towards the apex. The sustained maxima of the stems of the older plants offer strikingly parallel courses in circumference and number of bundles.

The data that have been compressed into these figures (Figs. 28–31) make it possible to calculate the width of a ridge at different horizons on the four stems; and this is given in Table 6. It is a small matter for the reader to multiply by five the figures of the right-hand half of the table to get the width of the circumference over a leaf-trace, which width has in literature the name 'vegetative line' of the axil. Though these widths do not give the actual width of the underlying ganglion and the leaf-trace (because of the narrowing radii) they indicate that the ganglion diminishes in size from the base of the stem to the distal end, and the leaf-trace with it. There must be a lag in the maximum of number of bundles following the maximum of circumference on account of the diminishing of the vegetative line, and that lag we observe in the curves of Fig. 32.

TABLE 6. *Average width in mm. of a ridge* (*left*) *and of that part of the circumference which covers a bundle whether common or cauline* (*right*), *for every decade of internodes of the stems nos.* 61, 62, 63 *and* 65 *from distal end to base* (*the few odd internodes beyond the uppermost decade have been added to that decade*)

	Width of ridge				Width of bundle			
Decade	Stem 61	Stem 62	Stem 63	Stem 65	Stem 61	Stem 62	Stem 63	Stem 65
91–100	—	—	—	0·30	—	—	—	0·16
81–90	—	—	—	0·39	—	—	—	0·22
71–80	—	—	0·60	0·46	—	—	0·32	0·25
61–70	—	—	0·53	0·52	—	—	0·30	0·28
51–60	—	0·24	0·61	0·67	—	0·15	0·36	0·34
41–50	—	0·45	0·65	0·65	—	0·26	0·38	0·35
31–40	0·51	0·50	0·67	0·71	0·28	0·30	0·38	0·38
21–30	0·61	0·55	0·70	0·73	0·33	0·32	0·38	0·40
11–20	0·73	0·66	0·66	0·78	0·39	0·40	0·40	0·41
1–10	0·76	0·77	0·78	1·16	0·43	0·45	0·41	0·46

The stem, no. 65, which to my regret could not be completely examined, was particularly vigorous; its 3rd internode had the phenomenal circumference of 44 mm. and held thirty vascular bundles, fifteen of each kind; but a large part of its thickness lay in the cortex as the 3rd was an underground internode; and the internode following had a circumference of no more than 18 mm. This illustrates the suddenness of the reduction in cortex at the level of the soil surface. From 18 mm. the circumference increased to 21 mm. at the 21st internode and then began to decrease. The succession of bundles expressed in pairs, common first, then cauline, was:

— 10–10 15–15 15–14 16–15 16–14 16–16 17–16 17–17 19–18
17–16 19–16 19–18 20–19 21–18 21–18 22–18 21–18 22–18 21–19
21–20 21–21 21–21 suppr. 21–21 21–21 19–19 21–20 21–20 21–19
21–20 20–19 21–18 19–16 21–19 20–20 21–20 21–20 21–20 21–20
20–18 19–15 19–15 19–16 20–17 20–18 20–20 20–20 19–19 20–20
20–20 20–20 20–20 suppr. 19–19 20–16 suppr. 19–18 19–18 19–18
18–17 20–17 20–17 19–17 22–19 21–17 22–17 22–17 22–17 22–17
21–17 suppressed,

and at this point the examination was broken off.

I have given these details because it was the largest stem that I have found and held the record number of bundles—forty-two (in the 22nd internode and repeated in the 26th). The circumference had passed its maximum several internodes earlier.

Of the five stems the following may be given as a collective summary: (i) that the greatest circumference, save where underground, was 17 mm.; (ii) that the maximum number of bundles was forty-two; (iii) that the greatest number of common bundles was twenty-two; and (iv) of cauline bundles eighteen, all these maxima being in the longest of the stems; (v) in respect of characters (i), (ii) and (iii), the next longest stem approached the maxima more nearly than any other. Further in summary: (vi) exact pectination was very unusual; but (vii) more usual in the base than at higher horizons; (viii) the excess of common over cauline reached seven, being 20–13, four times in stem no. 63 though never in two consecutive internodes; (ix) the cauline bundles showed a constancy at thirteen in stem no. 63, being unchanged from the 28th to the 74th internode, and over this part of the stem the common greatly outnumbered the cauline; (x) there was also a measure of constancy in stem no. 62 with the cauline at eight; (xi) the common bundles showed a small measure of constancy at thirteen in the early part of stem no. 61 and in the middle of stem no. 62; and lastly (xii) there was constancy towards the end of stem no. 64 at fifteen common bundles.

Constancy secures the establishment of a phyllotactic pattern; and the two that chiefly compete for retention are 3/8 and 5/13.

16. On the intervals between unbroken leaf-traces, here called interspaces

This section distinguishes growth at the apex into two parts, that which occurs before the provascular strands appear and that which follows. It deals also with the consequences that increase in number of bundles has on the number of internodes through which they travel.

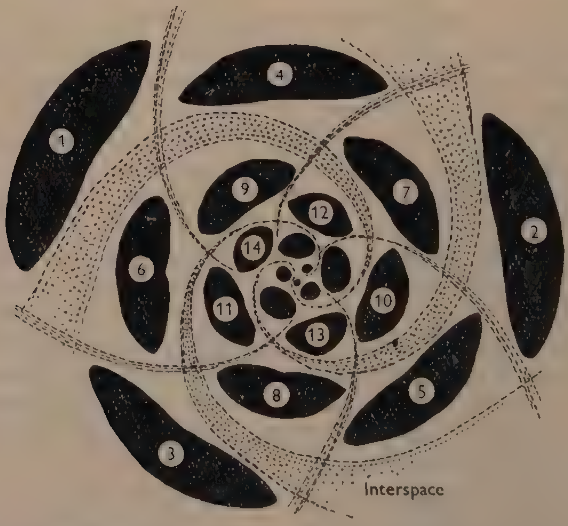


Fig. 33. Diagrammatic representation of an apex in the 5/13 phyllotactic pattern indicating contact-stichies expanded into interspaces. The emergences are numbered in the order of the genetic spiral.

In Fig. 13 (p. 334) leaf-traces of three successive leaves are indicated by the letters *A*, *B* and *C*. Between the leaf-trace of *B* and that of *A* run six of the twenty-nine vascular bundles in the stem; this means that a width that is $\frac{6}{29}$th of the circumference, overlies bundles having at the horizon of the section no connexion with the leaves *A* and *B* which they part. Another six bundles part B from C. Intervals between leaf-traces so vasculated I am calling *interspaces*. The reader will readily appreciate from Fig. 33 that they are widenings, or expandings if one so prefers, of the tissue between the foliar morphogenetic fields where there would seem to have been for a brief time genuine contact-stichies. Contact manifestly cannot but be brief.

My intention is to use 'interspace' here only in regard to transverse dimensions: expansion of contact-stichies in longitudinal dimensions produces internodes. Both are intercalations from the one source, namely the neutralizing of tissue between neighbouring morphogenetic fields as a consequence of their very essential property of self-centring and by it isolating themselves. From being neutral belts, the polarity of the plant shapes them through vasculation which is intensely polar. It will be evident to the reader that it is possible to ascertain the width of an interspace as readily as to determine the width of a leaf-trace by using the number of bundles. In post-formational development no sooner have the emergences, say of A and B in Fig. 13, become separated than provascular strands, first those belonging to emergence D and then those belonging to emergence G, provide the interspace with prospective bundles, annexing it in a measure from the influence of A and B to their own.

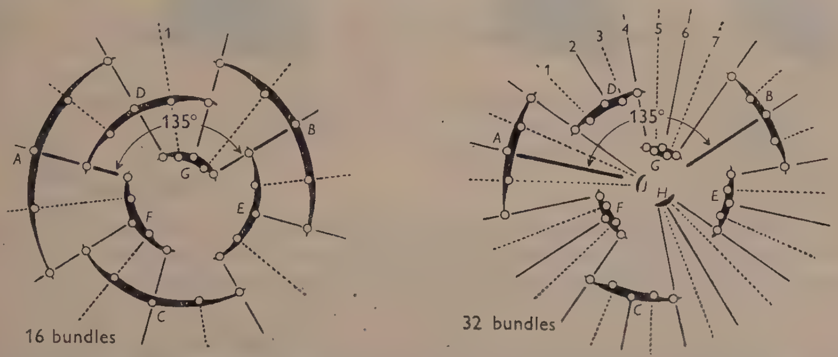


Fig. 34. Two phyllotactic patterns, both descriptively in the 3/8 pattern, yet widely different in the relation of the emergent leaves to the circumference. The diagrams give the courses of the bundles as if to the leaves though actually to the ganglia under them: the common bundles as continuous lines and the cauline bundles as dotted lines. The interspace between A and B holds one bundle in one diagram, but seven in the other.

At this point the terms of phyllotaxy become inadequate for they take no account of interspaces. Fig. 34 gives two diagrams, both of which writers on phyllotaxy, with justification from their point of view, describe as in the 3/8 pattern: yet they differ greatly; in the first a single vascular bundle threads the interspace, but in the other seven do so. In the first, that on the left, there is a ring of sixteen bundles: but in the second, that on the right, there are thirty-two. A stem of *Tamus* of the first would be 8-ridged, one of the second 16-ridged. With the leaf-trace constant at five bundles and the divergence the same (the angle is 135° in these two diagrams) they can only be unlike in the number of bundles in the interspace. As both patterns are possible in *Tamus*, it is essential to have terms for them; and they will be called '3/8 with eight ridges' and '3/8 with sixteen ridges'. One pattern is suitable only for slender axes, the other only for the thickest. The smaller cannot be converted into the larger without a

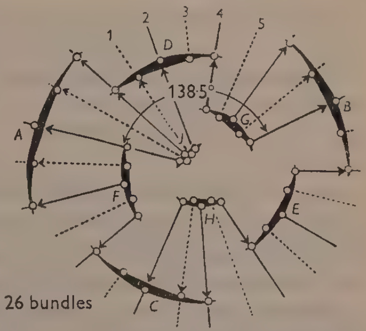


Fig. 35. A diagram in the 5/13 pattern for comparison with the diagrams in Fig. 34.

great deal of adding; and part of the way to conversion is through the 5/13 pattern. This is the pattern of Fig. 35, which is inserted here for comparison with Fig. 34.

Figs. 34 and 35 show that the most distant bundle intercepted by *A* in '3/8 with eight ridges' connects *A* with *F*, and in the other two connects *A* with *J*. Naturally, the wider the interspaces the more distant can be the interceptions. Fig. 36 is now inserted to show the relative sizes of stem to which the three diagrams of Figs. 34 and 35 are suited.

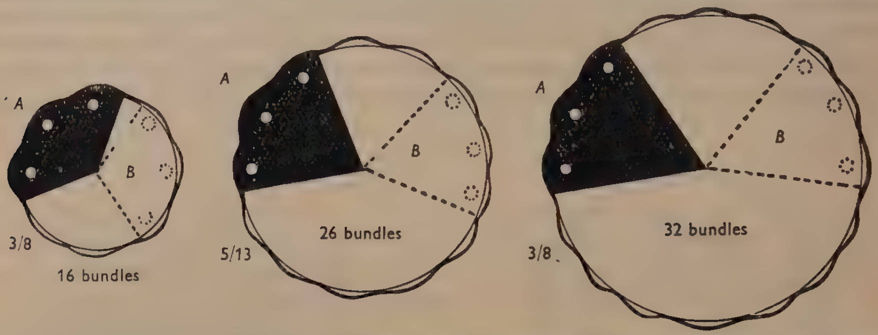


Fig. 36. A diagram to show the relative sizes that stems would have in the 3/8 pattern with eight ridges, the 5/13 pattern and the 3/8 pattern with sixteen ridges, on the assumption that the size of ridge is constant. *A* and *B*, two leaves; the appropriate interspace separates them.

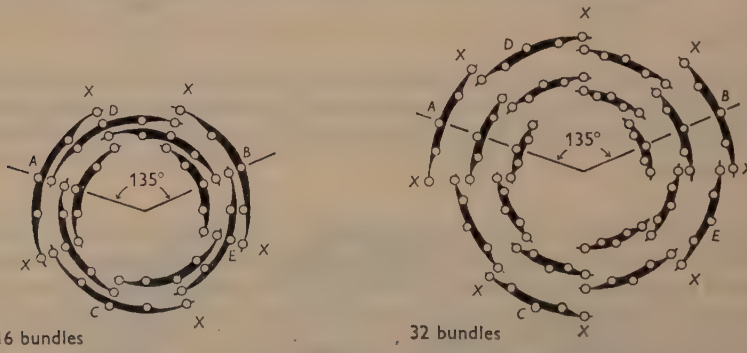


Fig. 37. Diagrams in the two 3/8 patterns with the positions where pairing can be introduced; five pairings in the left-hand diagram, eight in the right hand.

For the sake of simplicity no pairing of bundles has as yet been put into these diagrams, but common to cauline are in them 8 to 8, 13 to 13, and 16 to 16. The possibility of pairing will now be discussed.

Fig. 37 gives two diagrams of leaves in the 3/8 patterns with × at the points where pairing can be produced. In the left-hand diagram, if at the up-spiral end of *A* the mid-common of *D* misses the ganglion of *A*, it and the up-spiral common of *A* travel down the stem side by side as in Fig. 13 (p. 334). At either end of *A* and *B* and at the down-spiral end of *C* this pairing can be brought about and will then be evident in the internode under *A*. In the right-hand diagram, because the interspaces permit it, the possible number of pairings rises to eight. To complete the presentation of the argument, Fig. 38 gives the positions of possible pairings in the 5/13 pattern. Here again eight are geometrically possible. Anticipating a statement to be made in due place, it may be remarked that eight have never been found, but that seven have.

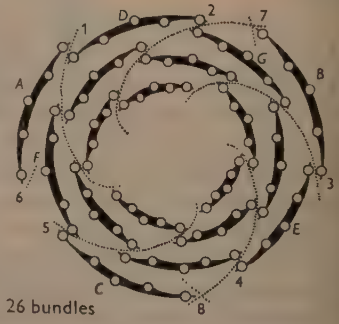


Fig. 38. A diagram showing the positions where pairing can be introduced in the 5/13 pattern, the number being eight.

Having pointed out that the 5/13 pattern is appropriate (Fig. 36) for a stem of a size between the two 3/8 patterns, it is perhaps well to explain why the possible number of pairings is as high as 8 in it instead of being intermediate. Fig. 38 does this by means of dotted lines indicative of the positions at which pairings can occur—namely five on the stichies conspicuous in the diagram and three by the mid-common of *F*, *G* and *H* missing the down-spiral side of ganglia where otherwise they should anchor.

It is obvious that insertion of all the possible pairings will leave the angle of divergence unchanged, as all sides of the stem will be equally affected. The missing of ganglia, by allowing bundles that do so to pass further down the axis than methodical arrest does, produces the results given in Table 7.

TABLE 7. *Number of internodes through which a bundle passes if it hits or misses*

Down-spiral common		Mid-common		Up-spiral common		
Hit	Miss	Hit	Miss	Hit	Miss	Ref. to figure
3	Cannot	3	5	2	5	34, component 1
3	8	8	Cannot	5	8	34, component 2
3	8	5	8	5	Cannot	35

Obviously missing is a consequence of growth occurring before the provascular strands secure anchorage and, the missing being at a ganglion, change in the number of bundles can take place only at a node, to the number of two, a miss at each margin. But we find greater changes near the bases of stems from hits, dispersed and irregular in number. These changes may involve a cauline as well as a common bundle. When a cauline misses, pectination is preserved.

While the opportunities for pairing must follow the genetic spiral, which is such as to distribute them to all sides of the stem in turn, it would be an extraordinary rapid increase in circumference that adds a pairing at every node and so keeps the balance. A rhythmic increase at a lesser rate, say one providing space for a missing at every third node, is more likely, and such would lead to lateral increase in the number of bundles; but the likelihood of any maintained rhythm is small, and observation shows that the changes are irregular.

Some writers, endeavouring to express their interpretation of previsual events at the apex, have suggested that the morphogenetic fields 'repel' each other. 'Repel', in that it infers movement, is the wrong word; isolate is right: the interspaces come into existence by reason of the self-centring of the fields.

17. THE KNOTTING TOGETHER OF THE VASCULAR MESH

A typical ganglion knots together ten bundles, the five that are those of its leaf-trace and five that extend to it from above. The simplest departures from type are the ganglia where pairing is introduced, because one of the five that should reach the upper side has missed and passed down the stem, and the ganglia where a bundle is eliminated by the arrest of six. Near the base of a stem change is often more rapid so that the number entering the upper side of a ganglion is more than six. Otherwise the mesh is geometrically constructed. Add together the number of internodes through which the five bundles of the leaf-trace severally pass and the total is the sum of the bundles in the internode of the horizon. Express this in reverse—by counting the number of bundles to be seen in a transverse section, a measure of the length of the mesh is given. The data which bear this out are in Table 8, and are derived from Figs. 35 and 36.

With Table 8 before the reader, I would call his attention to the way in which a stem of the lowest line of the table has all its leaf-trace extinguished at the same level, namely in the ganglion of the 8th node below; below this ganglion another leaf-trace occupies the same width of the stem which is therefore vasculated ribbonwise; I call attention because I suspect that the fasciation which is so common in the stems of *Tamus* may be promoted by this happening. If that be right any tendency in the species to larger stems finds here a limiting factor.

TABLE 8. *The number of internodes through which the bundles pass in the following phyllotactic patterns*

	Bundles of leaf-trace					
	Down-spiral			Up-spiral		
Pattern	Common	Cauline	Mid-common	Cauline	Common	Sum of line
3/8 with 8 ridges	3	3	3	5	2	16
5/13	3	8	5	5	5	26
The same with max. no. of pairings	8	8	8	5	5	34
3/8 with 16 ridges	3	8	8	8	5	32
The same with max. no. of pairings	8	8	8	8	8	40

Within my experience no bundles extend beyond eight internodes: for *J* (of a sequence) to anchor in *A* (of its sequence) is common; *K* would not, as being towards the other side of the stem; *L* and *M* do not; they are extinguished earlier. To explain my interpretation of eight being the limit I have prepared Fig. 39. The reader has before him in it a plan of the bundles of the 5/13 pattern as they would lie if the stem were cut open longitudinally and opened out with the cortex downwards. In this figure it looks easy for, say, the mid-common of *J* to pass between the bundles numbered 5 and 6, both being common and so to raise the pair to three; but this never happens. I interpret the failure physiologically,

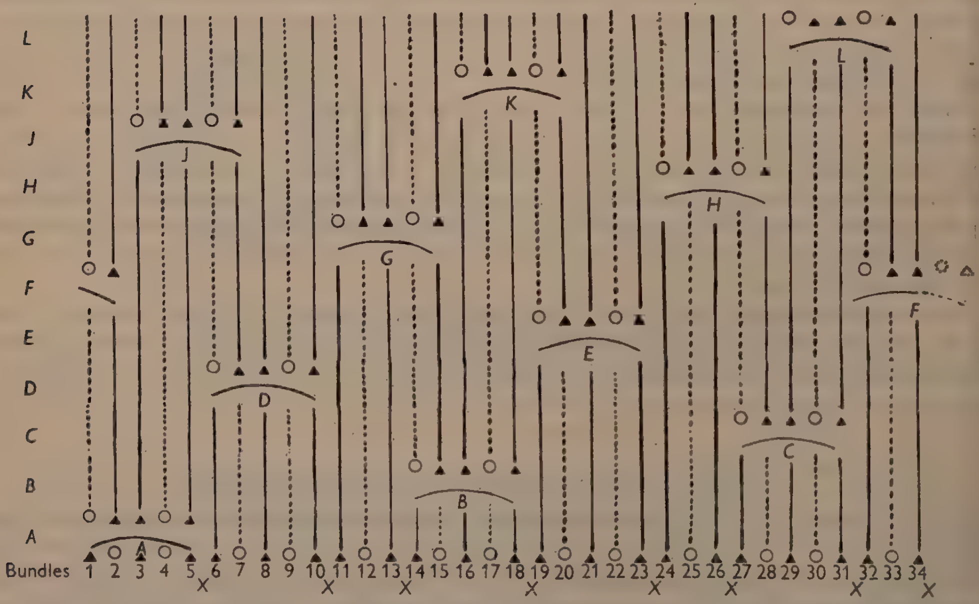

L
K
J
H
G
F
E
D
C
B
A
J
K
G
D
B
E
H
C
L
F
Bundles 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34

Fig. 39. The vascular bundles of a stem with the 5/13 pattern to which all the possible pairings have been added, as the bundles would lie if the stem were cut open and unrolled with the cortex downwards.

assuming an incompatibility, at the time when unions are made, between ganglia so far apart; and I refer my reader to my paper on the vasculation of the leaf of *Tamus* (*J. Bot., Lond.*, 1939, p. 329) for the observations which led to this interpretation. In that paper a very accurate drawing of the fine nerves of the leaf was given suggesting that little nervules make junctions with slightly larger nervules, but are unable to do so with nerves obviously larger and demonstrably formed earlier. If the interpretation be right then eight nodes make the maximum unit of apex with a measure of compatibility. The unit may be less than eight, perhaps, in plants that have not strengthened their stem.

The inability of the stem to associate together more common bundles than two causes patterns such as those in Fig. 40 never to appear. Ortho-tristichy, for instance, cannot be led into by a dropping of bundles one by one up to the extinction of the interspace. These two impossible diagrams, for the purpose of illustration, have been left with considerable interspaces. The plant itself shows that as ortho-tristichy is approached towards the end of the stem, the interspaces dwindle in size; and the last stage is in the nature of a leap.

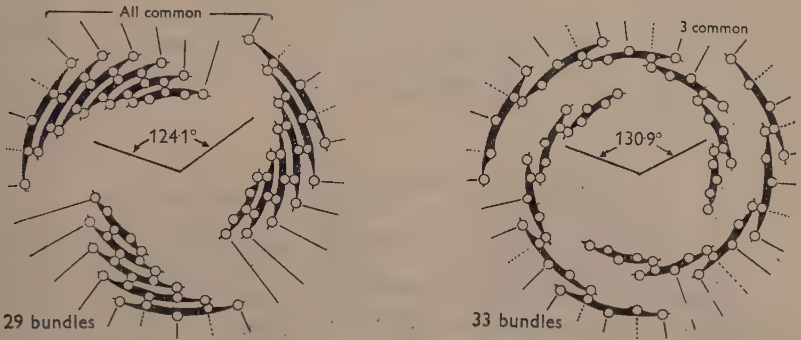


Fig. 40. Two of the many patterns geometrically possible, but not realizable.

The geometrical exactitude of the relation of the length of the mesh to the number of bundles in the stem shows that the mesh is extended through more internodes the greater the thickness of the stem.

Up to this point I have been occupied in describing the escape of bundles from arrest; I turn now to the way of their arrest; and I use a selected stem to illustrate it by what happened in the neighbourhood of three of its nodes, the 5th, 6th and 8th from the base. Fig. 41 (left) is of the 6th or node of *F*; that in the centre of the 5th or node of *E*, and that on the right of the 8th or node of *H*. The stem was taken when very young and serial sections were cut. Of its several nodes the three used were found the most instructive. I start with the diagram derived from *F* as being a little simpler than the others. The base of the petiole is indicated in outline in the centre and the bundles that enter or leave its ganglion are seen as if through this base. The arrow through it indicates the direction of the genetic spiral. The ridging of the stem is indicated above and below the petiole. Common bundles are indicated by continuous lines: cauline bundles by dotted lines. Of course when bundles are not disposed in the same way above and below a node the exact course of the ridges is altered; but about *F* there was scarcely any alteration in the ridges. The margin of the ganglion was approached on either side by a cauline bundle: of that on the down-spiral side the whole was adsorbed; of that on the up-spiral side one-half. At the ganglion of *J* the cauline on its down-spiral side was similarly adsorbed, so that the upper side of the ganglion lost one entrant bundle; laterally it gained two. By this it was caused to be a knot linking eleven bundles. The diagram further shows a cauline from *L* dwindling away. The total result was that the strip of stem had, at the top of the diagram, thirteen bundles and at the base eleven, for nos. 3 and

5 on the right-hand side of the figure had disappeared, the one from dwindling away, the other from unusual adsorption.

Turning to the central diagram, i.e. to the neighbourhood of ganglion *E*, adsorption of a bundle (split) occurred in the same position as in *F*, and there was adsorption on the margin of *G* which robbed *E* of an entrant bundle. Just above *E* the bundles over

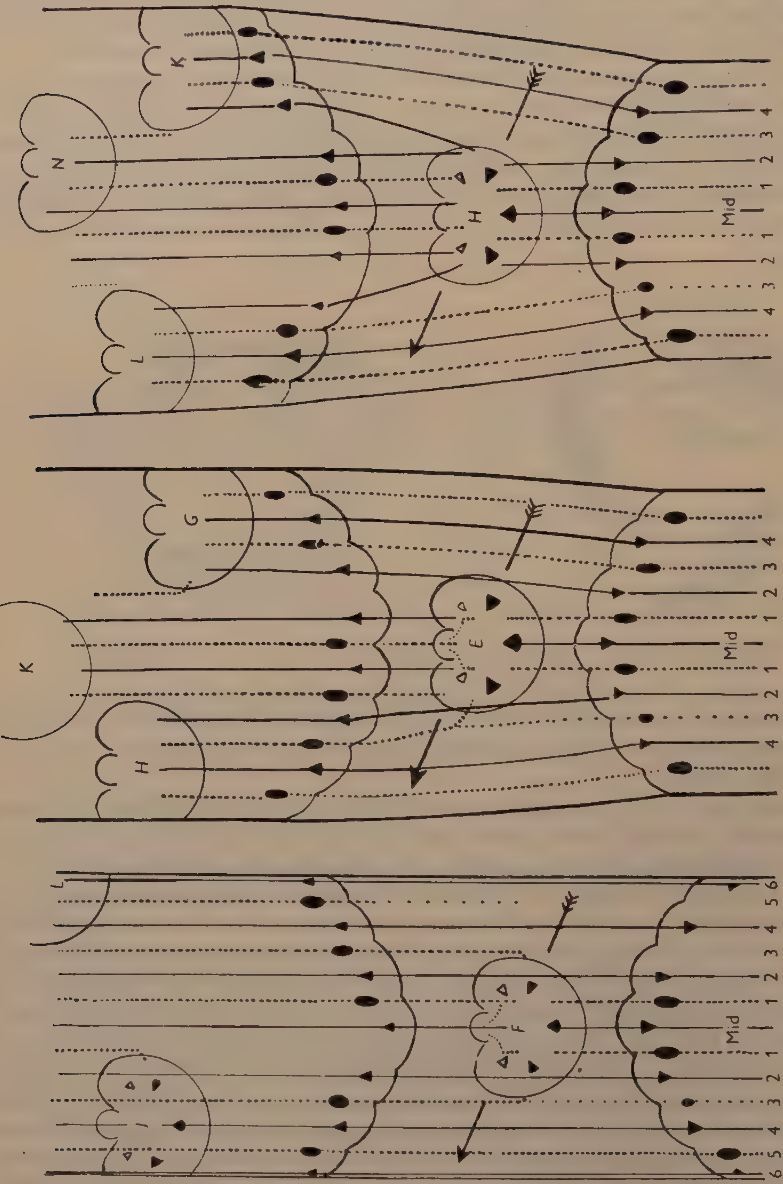


Fig. 41. Left: the course of bundles in the neighbourhood of ganglion *F* of a selected stem. The emergence *F* is central and an arrow through it gives the direction of the genetic spiral; scalloped lines above and below suggest the ridges of the surface; continuous lines indicate the common bundles and dotted lines the cauline. Arrests of bundles at the margin of the ganglion, the splitting of a bundle and the fading out of another are seen. In the centre a similar diagram of the horizon of *E* and, on the right, another of *H*.

this strip of stem were twelve in number, below eleven; and it happened here that the bundle which occupied the centre of the diagram above *E* was a cauline bundle but below a common bundle. Such interchanges are very abundant; they are scarcely noticeable to the eye from their smallness and because under the principle of equidistance the plant obscures them. The ganglion of *E* knotted together twelve bundles, seven descending to it from above, while below there were of course the five of the leaf-trace.

Proceeding to comment on the right-hand diagram, i.e. to the horizon of *H*, two unusual adsorptions are seen, one at the margin of *L* and one at the margin of *K*, both leading to pairing of common bundles; and the ganglion of *H* received both pairs whereby it knotted together twelve nerves, seven that descended to it and the five of the leaf-trace from it.

It is by irregular happenings such as these that the rapid increase in the number of bundles at the lower end of a stem is contrived. They make the mesh irregular but the maximum distance that a bundle travels is all the same through eight internodes.

18. THE DIVERGENCES CONSIDERED AS FORMING A PROGRESSION

As already pointed out it is a minute axis which, while within the perennial bud, gives origin to the calyptra; and the calyptra outgrows it, hoods it and envelops it. The ability of this emergence to grow against the axis is obvious; but the ability lasts only for a time. Meanwhile, the axis strengthens and has space for another emergence. It is the business of the axis to initiate emergences; and we must think that it is restrained until there is room for this second emergence; the restraint disappears when there is room at a divergence of 180°, the maximum possible—180° along angle ϕ; though there is a little more room than 180° implies because the real angle is θ. This second emergence, produced in order to be scale-leaf *A*, is presently followed by that for scale-leaf *B*, which likewise may be at a divergence of 180°. Accordingly, in the first component of Fig. 42 I have drawn the diagram which would result from a succession of emergences appearing at 180°. There would be ten bundles in the stem, five from each leaf-trace; and the stem, being distichous, would have its sides in no vascular connexion with each other. In the second component of that figure I have increased the circumference by 20 % so that we get interspaces; but there is no means of vasculating them. In the third component I have again increased the circumference by 20 %, assuming the emergences to be of constant size and the increase of the circumference to pass into the interspaces, which still can receive no vascular bundles. In the absence of vasculation these second and

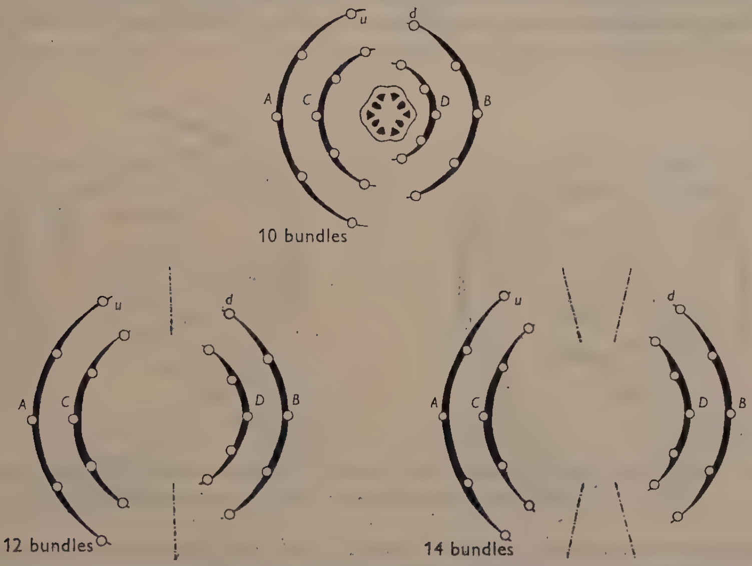


Fig. 42. Three hypothetical diagrams, the second 20 % greater in circumference than the first and the third 20 % greater still. Explanation in the text. *u*, up-spiral margin of interspace; *d*, down-spiral margin, when genetic spiral has arisen.

third components cannot be realized; and the first could not progress to them from th want of cross unions. Spirality or spirotrophy enters. In the first component of Fig. 4 I have hypothetically allotted 20 % of the increase in circumference to the introduction of spirality and left the other 20 % for interspaces. To make the explanation as simple as possible I have disregarded the largeness of the ganglion of scale-leaf *A* and exclude the calyptra from consideration; but I shall return a few lines below to the consequence of the largeness of the ganglion of scale-leaf *A*. Meanwhile, the consequence of the introduction of spirality is that vascular bundles are provided for the interspaces; and the condition of Fig. 42 is converted into that of the first of Fig. 43, representing fairly well what spirality leads to in the plant. Spiro-distichy results, and fourteen bundles as soon as the interspaces are two; thirteen in the internode preceding. The divergence with fourteen bundles is 154°. It is a great reduction from the divergence of 180° with which an axis starts its business. This rapid reduction is aided by the large size of the ganglion of scale-leaf *A*, wherein three-quarters of the bundles descending find anchorage. The reader is now referred to the second component of Fig. 43 where he will observe scale-leaf *A* given its approximate excess proportions. To make this diagram as near the actual as I can, I have provided no interspace between *A* and *B* (*u* to *d*), but enough interspace

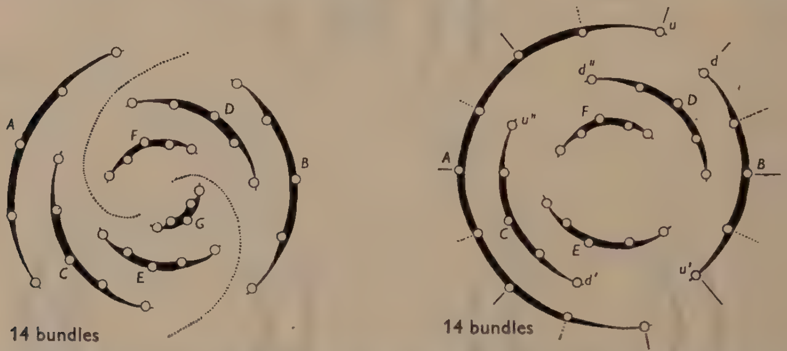


Fig. 43. Diagrams of the introduction of spirality: that on the left hypothetical; that on the right allowing to scale-leaf *A* its proportionate size.

for the passage of one bundle between *B* and *C* (*u'* to *d'*) and again between *C* and *D* (*u''* to *d''*). The great size of this specialized ganglion, that of *A*, neither helps nor retards spirality, but helps the stem to increase the number of bundles with (as regards the number of nodes) rapidity. Thus it is demonstrable that spirality is a necessity to the stem, introduced into the routine as soon as there is room for it, and is essential for bringing unity into the mesh.

So far this spirality has the form of spiro-distichy. It begins to pass over to spiro-tristichy at about sixteen bundles (Fig. 44). In the transition between distichy and tristichy, pentastichy based on two turns of the genetic spiral appears. This is why pentastichy appeared in Figs. 26 and 27 at the appropriate distance from the base. One may comment that it would not be amiss to use different terms for the two kinds of pentastichy that plants show. This kind, on two turns of the spiral, is the foundation of the calyces of a great preponderance of the dicotyledons.

Figs. 26 and 27 have shown this pentastichy changed into tristichy, and Table 5 (p. 348) has indicated that after the change the divergence must retain tristichy in some form as the angle tends to narrow towards 120°. The small diminution at maturity of the vegetative line set against the more considerable increase (again at maturity) of the circumference, demands in proportion a slightly more considerable increase in the size of the interspaces (at maturity) over that part of the stem which is below the horizon of greatest circumference. Then beyond this horizon comes, with the decrease of the circumference, a decrease in the size of the interspaces, accompanied by only a very small decrease in the width of the vegetative line. It is to be noted that the vegetative line is more nearly standardized than the other factors in the case and this is because the growth of emergences is more regular. On the up-grade in circumference the number of bundles increases with the size of the interspace until something like the first component of Fig. 45 is built. Then follows the diminishing represented in components nos. 2 and 3, wherein tristichy is preserved to the end of the ordered stem. In the tip where it dies, the order is broken up.

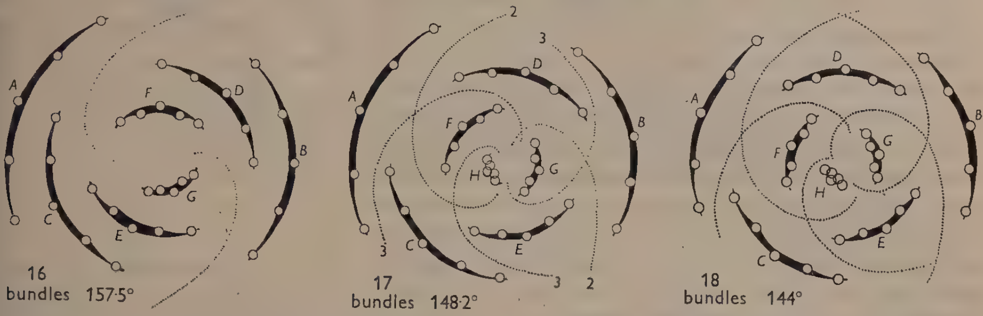


Fig. 44. Diagrams indicating where expansion of the stem leads spiro-distichy into spiro-tristichy, with conflicting stichies (numbered 2 and 3 in the central component).

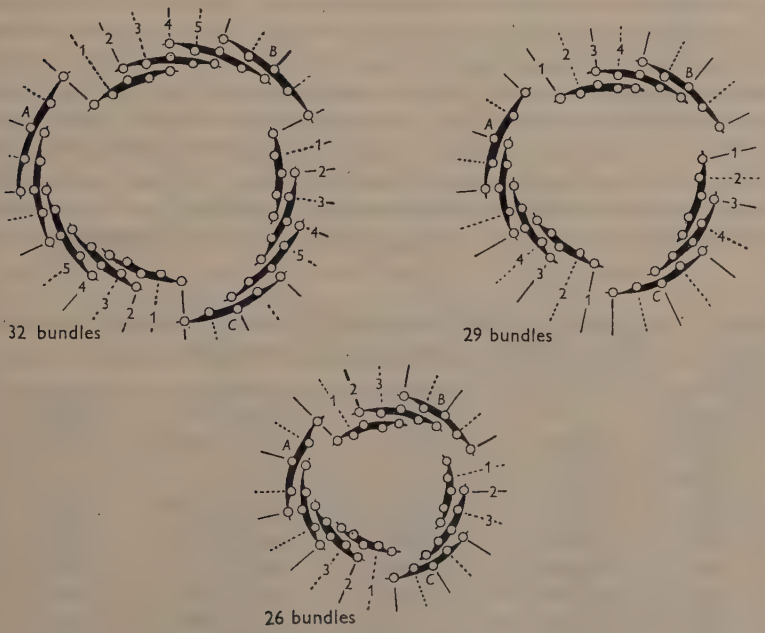


Fig. 45. Diagrams of the patterns underlying the diminution of the stem from its greatest circumference.

To ascertain what happens in the dying tip I took in the month of September a still-living stem-end and examined it in serial sections. Fig 46 shows what was found. At the lowest internode of the series the stem was 8-ridged, three of the ridges over the leaf-trace of *A*, three over that of *B* and two over that of *C*. The divergence had been narrowed to less than ortho-tristichy and a cauline bundle from *C* was missing. The internode between *B* and *C* was 6-ridged, two of the ridges being closely approximated. The internode between C and D was 5-ridged with the same two ridges closely approximated. Leaf E was almost opposite to D and its two cauline bundles were missing.

The missing cauline bundles and the considerably displaced leaf E were all on the side of the stem over the last fully developed leaf of the stem, the leaf that came before A; but that this by its autochthonous growth had interfered is not demonstrated though it is a possibility. Some of the bundles traversed no more than one internode.

It is exceptional for stems reduced to this condition even to live and, if they do, they exist without growing.

The progression which has been outlined of the divergence in the stem from end to end is basic and built on by the pairing of common bundles and would be more evident than it is if paired bundles were not of almost invariable occurrence in variable numbers. I estimate that of every 100 internodes only thirty repeat the numbers of common and cauline that were in the internode before. Of the rest, say, 55 % differ by one unit and about 12 % by two units, the few over by more than two. Thus change is the rule. It is made rapidly in the lower part of the stem.

Because it is desirable to illustrate the rapidity I selected an average stem and from it drew the data in Table 9 which shows that the bundles increased jerkily over the fifteen lowest internodes by sixteen (from thirteen to twenty-nine), the rate greatest above D, at E and F. As the second column shows, E and F were just above the internodes that attained the greatest length; but the laying down of bundles long preceded the elongation and cannot be recognized as connected with their lengths directly. The Table gives the diameter of the stem and the diameter of its stele; and the position where the cortex ceased to be thick is found rather below these internodes. Neither the elongation of the 4th and 5th internodes which was stimulated by the spring push, nor the thickening of the cortex which arose out of an underground position, had anything to do with these changes.

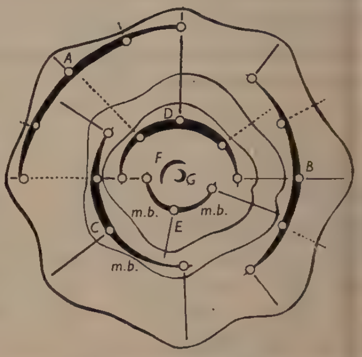


Fig. 46. The diminishing vasculation of the exhausted stem-end figured as no. 18B (p. 341). *m.b.*, missing bundle; further explanations in the text.

TABLE 9. *The diameters of internodes and the number of bundles, etc., in the fifteen lowest internodes of a selected stem*

Internodes						
Serial no.	Length (mm.)	Diameter	Diameter of vasc. stele	No. of bundles (in brackets common-cauline)	No. arrested at ganglion named	No. of ridges
15	19	3·6	3·4	29 (16–13)	7 *O*	15
14	46	3·4–3·6	3·2–3·4	27 (14–13)	6 *N*	14
13	67	3·2–3·4	3·0–3·2	26 (13–13)	5 *M*	13
12	19	3·0–3·4	2·9–3·2	26 (13–13)	6 *L*	13
11	64	3·0–3·4	2·9–3·2	25 (13–12)	5 *K*	13
10	78	3·0–3·4	2·9–3·2	25 (13–12)	6 *J*	13
9	30	2·9–3·4	2·7–3·2	24 (12–12)	5 *H*	12
8	76	2·9–3·2	2·7–3·0	24 (12–12)	6 *G*	12
7	38	2·9–3·2	2·6–3·0	23 (12–11)	5 *F*	12
6	83	2·9–3·2	2·5–3·0	23 (12–11)	8 *E*	12
5	236	2·9–3·2	2·5–3·0	20 (10–10)	9 *D*	10
4	262	2·9–3·2	2·0–2·2	16 (8–8)	6 *C*	8
3	76	2·9–3·2	2·0–2·2	15 (8–7)	6 *B*	Obscure
2	31	2·9–3·2	1·5–1·8	14 (7–7)	6 *A*	Obscure
1	8	2·9–3·2	1·5–1·6	13 (7–6)	—	Obscure

The Table shows that tristichy was already developed at the 5th internode, so that the shaping illustrated in Fig. 44 (its second and third components) had been run through at the 5th node; one may say of it rapidly, if the rate be measured in nodes; though as the season was winter, growth was not rapid at the time.

Pairing is always less abundant at the base of a stem than higher up; and up to the 13th internode there were as many internodes with the bundles exactly pectinated as with them imperfectly so. In stems, as a whole, imperfect pectination is the rule, as the following statement (Table 10) shows. The four stems used in making it, nos. 46–49, had, as their most usual number of pairings, three to an internode. Tristichy should favour three or none or six, and demonstrably favours three. It will be observed that the last of the four stems held more pairings than the others, but this does not imply a corresponding greater tendency to initiate pairs so much as the retention through a series of internodes of pairs once formed.

TABLE 10. *A complete census of the internodes of the four stems, nos.* 46–49, *showing how many had no paired bundles and how many had* 1–7 *pairs*

Stem no.	No pairs	1 pair	2 pairs	3 pairs	4 pairs	5 pairs	6 pairs	7 pairs
46	4	8	12	15	—	—	—	—
47	0	2	16	20	10	7	—	—
48	8	19	23	23	15	5	—	—
49	4	5	10	24	12	13	11	4

As the divergences make a progression from the base of the stem to its distal end, not subject to alteration by the growth which causes the maximum circumference to be some way above the base, this latter growth is of a period too late to influence the spacings that the foliar morphogenetic fields assume, these spacings having already been determined in accordance with the strength that the axis had obtained. But this growth on which the horizon of maximum circumference is determined precedes the appearance of the provascular strands, for it determines the number of them that thread the interspaces; and this assures us, if assurance be asked, that the phyllotactic pattern is made before the influences work that create the increase to the circumference, and that the pattern is stabilized.

19. THE LENGTHS OF THE INTERNODES

It was very unexpected to find that the length of the internodes is greater if the ganglion be on one side of the stem than if it be on the other. The evidence will be given in this section after the seasonal effects have been discussed.

In 1935 I selected thirty-six stems from various habitats in the neighbourhood of Paignton, Devon, endeavouring to cover all the usual conditions in which *Tamus* was to be found by equal numbers of male and female stems. Every internode was measured and the measurements analysed in various ways. It was found that the application of a moving average based on five internodes at a time, by smoothing the curve, brought out seasonal behaviour. The curve was found to rise sharply to an early peak, then to fall less abruptly; after that to rise again slightly and finally to fall in a very marked manner to the end of the stem's growth. The results were reported in 1936 (*J. Bot., Lond.*, pp. 153–63): on p. 154 the complete data for one of the stems were given and on p. 156 a compound curve made after analysis. The reader is provided in Fig. 47 of this paper with another complete curve which shows the early abrupt rise; but it does not show a second rise, and I have come to the conclusion that the second rise, which was quite evident in stems of the season 1935, had depended on variable conditions and is not a part of the plant's annual cycle. The two peaks of the curves drawn in 1935 were called respectively that of the spring push and that of the summer growth; the latter which I now regard as a climatic effect will not be discussed along with the other features. The part of the curve following the peak of the spring push was called the waning of the spring push. After it follow summer growth and exhaustion. The spring push is invariable, as a brief abrupt effort which is never extended, but wanes deliberately; the summer growth is spread out; the exhaustion is rather rapid and terminates abruptly.

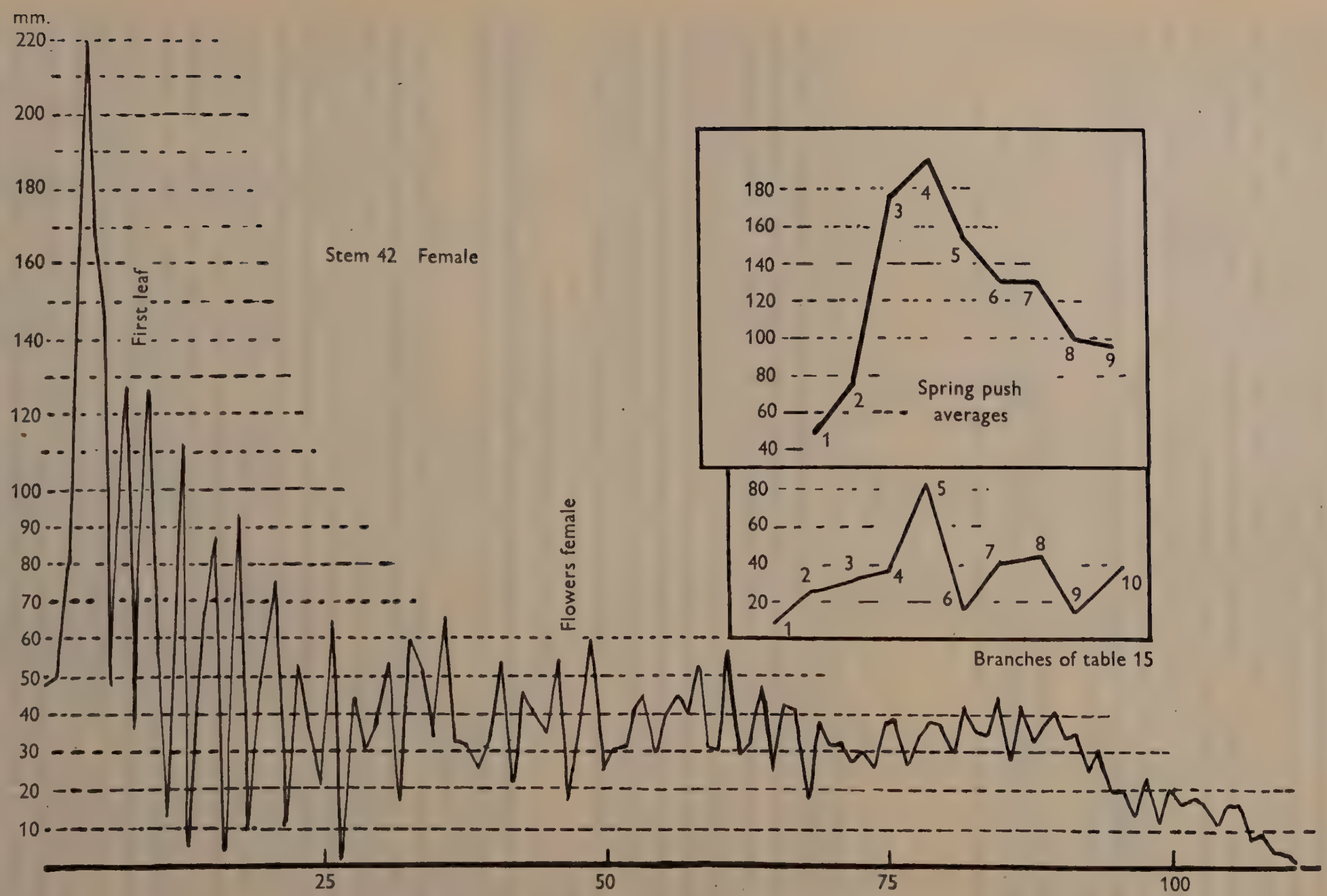


Fig. 47. A graph of internodal length along the whole of stem no. 42, a typical stem, though handicapped in earlier growth by heavy shade from the foliage of the late-trimmed beech hedge in which it grew. Lengths in millimetres. *Inset.* Two graphs, one average lengths of the early internodes of all the stems measured; and the other, average lengths of the lowest internodes of the longer aerial branches from three stems of a much branched plant. Explanations in the text.

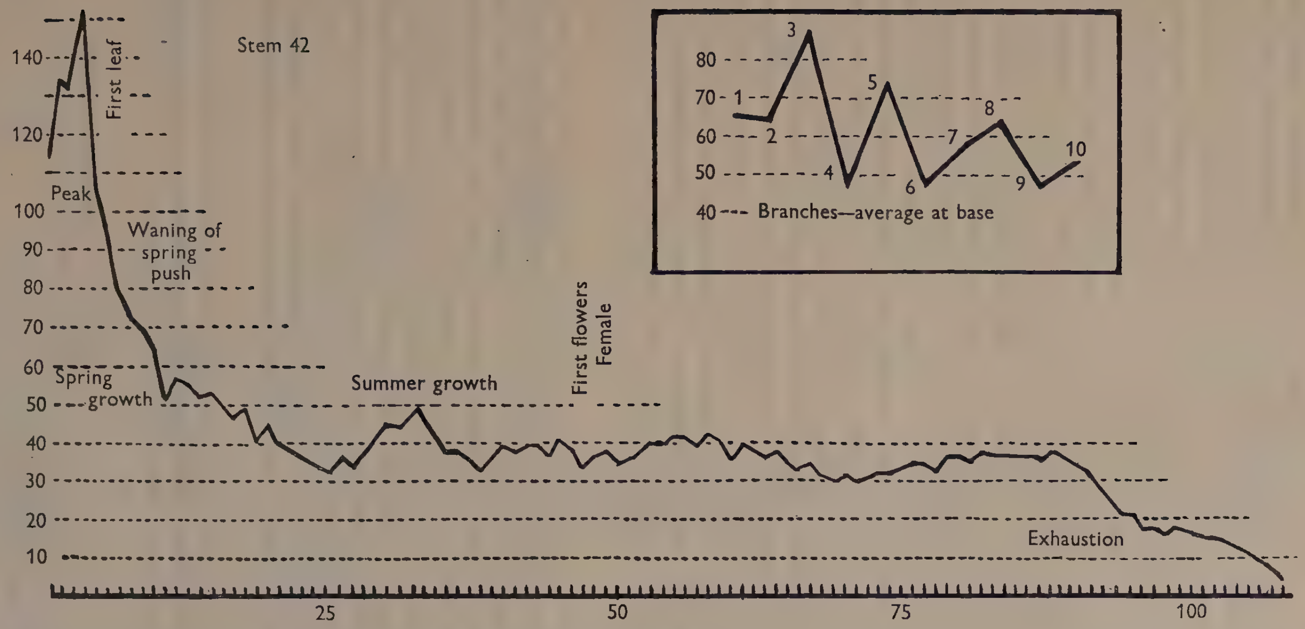


Fig. 48. The graph of Fig. 47 smoothed by a moving average, based on five internodes at a time, each average assigned to the middle internode of the five. The graph is classified seasonally. *Inset.* The average length of the lowest nodes of branches caused to develop by decapitation of stems; see text, p. 371.

The first step in analysis of the curve in Fig. 47 was to apply a moving average by units of five and this gave the curve of Fig. 48.

The figures may be said to show two exhaustions, one that of the spring push and the other of the annual growth. These exhaustions are on average lengths and leave the deviation from average to be explained. At first sight this deviation shows little indication of underlying causes. The stem no. 42, which provided the data for Figs. 47 and 48, was examined in the autumn of 1944 after all elongation had ceased. It had been produced in a beech hedge of my garden, through which it had grown; and it had been very heavily shaded in its lower parts until the hedge was trimmed, so heavily that some of its leaves had died after expanding; but when the stems (there were three from the one tuber and this was the furthest in) had grown so as to overtop the hedge they received no shortage of light. Seeing in this innermost stem definitely adverse spring conditions and wishing to lay before the reader a curve contrasted with the stem grown under favourable spring conditions I have employed it for Fig. 47; and the reader, if he cares to compare the curves, will note the absence of a summer peak in the curve of this figure (Fig. 47).

I do not need to give the absolute measurements incorporated into Figs. 47 and 48. The existence of the spring push, of its waning, of the summer growth with or without modification from favourable weather in spring, and of the exhaustion period are proved; and the next step is to work from a base-line provided by average lengths with the object of studying the deviation from average. A moving average on five units has sufficed so far, but has the obvious disadvantage that any succession of short-long-short-long-short is not smoothed, as three longs fall into one group and three shorts into the next. A moving average on a larger group of units has the disadvantage of throwing out more than two units at each end, so that there is an absence of data for the very base of the stem where, owing to the rapidity of change, possession of data is most desirable. I have tried larger groups of various sizes and finally used in Fig. 49 three, one of five, one of eight and one of thirteen, summed them and employed the mean as my base-line for deviation.

The stem of Fig. 49 is not no. 42 which was used for Figs. 47 and 48, but stem no. 50; not that no. 42 was unsuited (it was indeed one of the stems worked on, see Table 11, p. 370), but to vary seemed profitable. Down the centre of the figure are the three interpretations by different moving averages; above and below, the round dots give the excess or deficit of the internodes in length from the mean of the three averages. The mean is not drawn in. Internodes nos. 1–6 precede the possible use of the moving average on thirteen; and a similar number of internodes are beyond its use at the other end: in the graph whatever could be used has been used. But in the supplementing calculations of standard deviation, the six basal and seven distal internodes were excluded, as being beyond the limits of the moving average by thirteens. Unfortunately the exclusion of these means exclusion of the peak of the spring push, as well as the extremity of the zone of exhaustion. It must be so.

Inspection of Fig. 49 suggested to me that in the middle there might be a zone of reduced variability; the figure will suggest it to the reader; so standard deviations were calculated on this stem as of three parts, with this result:

	Standard deviation
Waning of the spring push, internodes 7–33	28·5
Middle part, internodes 34–52	11·8
Distal part, internodes 53 to the end	10·4

and the division into three was not borne out. I drew graphs for other stems and they did not support it; but all showed a standard deviation of the waning of the spring push consistently higher than that of the summer growth, i.e. that the deviation is intensified during the spring push in the elongation effort. The data shown in Table 11 were obtained

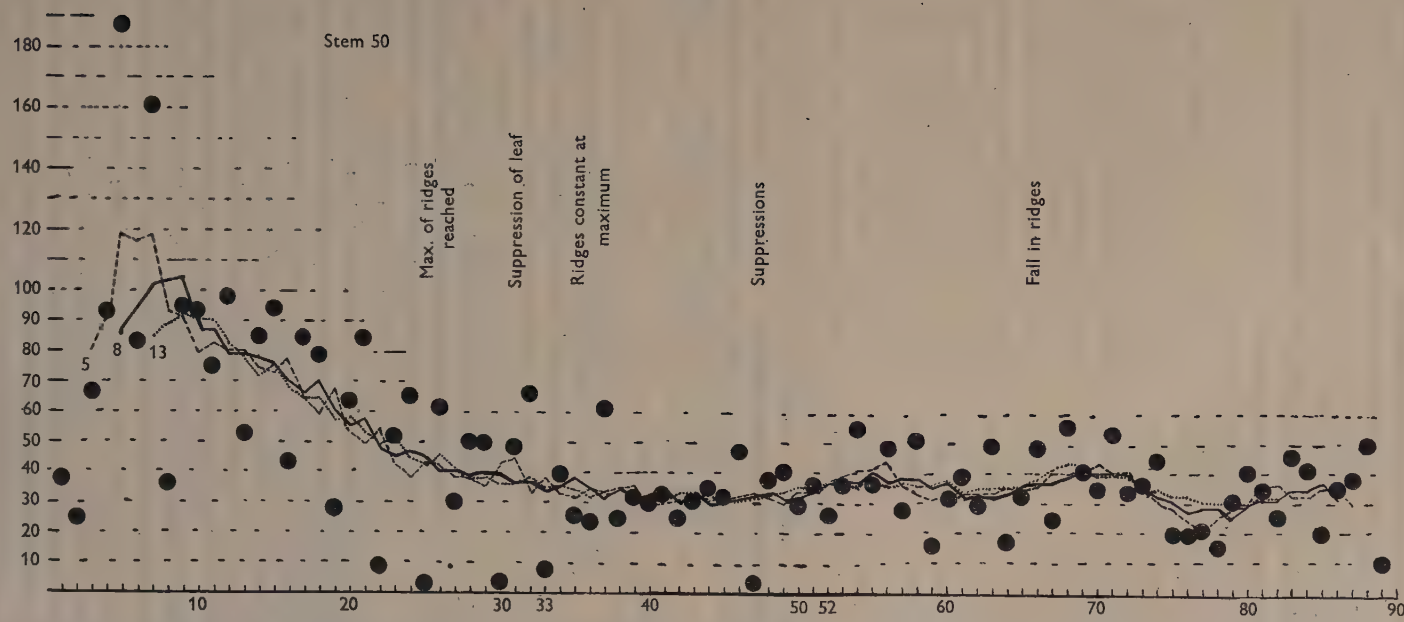


Fig. 49. Graph of the deviations from average of all the internodes along stem 50. Centrally in the graph are three curves, one by a moving average on groups of five, another on groups of eight and a third on groups of thirteen. The deviations from the means of these, in millimetres, are given in the dots (above if in excess; below if in deficit). Ordinates in mm.: abscissae the successive internodes.

by examination of nine other stems by the same method. The Table shows a constant excess in the first part over the rest, an excess that may be considered as in some way a consequence of the spring push. The difference is least in the plant only just mature.

TABLE 11. *The standard deviation of the length of the internodes of nine stems from various localities divided at the end of the waning of the spring push*

	Waning of spring push		Summer growth		
No. of stem	Nos. of internodes	S.D.	Nos. of internodes	S.D.	Origin, etc.
44	(7–20)	40·8	(21–51)	17·5	Leatherhead, 1944, a stem with many suppressions in it
14	(7–41)	40·7	(42–82)	10·0	Paignton, 1935, on deep soil
42	(7–27)	37·4	(28–107)	9·2	Leatherhead, 1944, from a dense beech-hedge
13	(7–41)	30·4	(42–76)	6·9	Paignton, 1935, on deep soil
16	(7–29)	27·3	(30–41)	12·1	Paignton, 1935, a plant that had lost the top part of its stem
17	(7–28)	24·0	(29–41)	13·2	Paignton, 1935, a twin stem of the last
47	(7–28)	24·8	(29–107)	19·7	Leatherhead, 1944, a stem robbed of sunlight from S. and W. by palings
15	(7–25)	17·3	(26–44)	5·9	Paignton, 1935
49	(7–18)	10·1	(19–37)	7·8	Leatherhead, 1944, a plant just mature

I have given in Fig. 22 (p. 344) a diagram of the phyllotaxy of stem no. 50 and have now in Fig. 49 supplied data of dispersions in it. Drawing what is required from these two I produce conclusive proof in Fig. 50 that the deviations are lateral on the stem. Fig. 50 is the phyllotactic diagram of the first part of Fig. 22 with the deviations set against the several foliar organs.

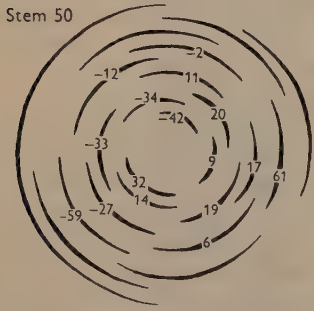


Fig. 50. Diagram repeating from Fig. 22 the positions of the lowest foliar organs on the stem and adding the deviation in length from average in this part of the stem of the internode below each of these foliar organs.

The deviations in deficit are on the side of scale-leaf *A* while those in excess are on the calyptral side. The greatest excess is 61 and is above the calyptra; the greatest deficit is 59 and opposite to the bud of the calyptra.

I grow in my garden a vigorous race of *Salvia sclarea* Linn.; the bracts along the branches of its robust inflorescences are decussate, with the first pair athwart the axil, and the next pair towards and away from the parent stem, and so forward; the flowers are invariably more numerous in the axils of the bracts that are away from the parent axis than in axils of those towards the parent axis and the bracts that are athwart are much more developed away from the parent stem than towards it. I make reference to this *Salvia*, the condition of which is by no means unusual, to illustrate the condition of *Tamus*. The determinant in *Salvia* comes from the parent stem, and the effect is in the branches. I have been careful to show earlier that every stem of *Tamus* is a branch; and I have pointed out above that the plus and minus sides of the lower part of the stem are those of the calyptra and scale-leaf *A*; these being in relation to the calyptra of the parent axis, in the axil of which the bifacial stem appeared, such that the plus side is adaxial, not abaxial as in the *Salvia*. But all the same a quality in which the stem has plus and minus sides of this nature was most unexpected.

This dorsiventrality extends along the whole stem as witness the serrations of the graph (Fig. 47). I endeavoured to assure myself that the side is constant; but it was not possible to make certain; though I believe that it is constant.

There is a quick way of detecting the presence of these plus and minus sides dependent on assuming what the divergence is. Let inspection suggest a pattern of 5/13 to occur on part of a stem; then arrange the internodal lengths along thirteen orthostichies and sum the columns. Plus and minus sides appear distinctly in trials such as in Table 12.

TABLE 12. *Lengths of internodes arranged in thirteen orthostichies, the number appropriate to a 5/13 pattern, showing plus and minus sides—illustrated by two cases*

	1st, 14th, etc.	9th, 22nd, etc.	4th, 17th, etc.	12th, 25th, etc.	7th, 20th, etc.	2nd, 15th, etc.	10th, 23rd, etc.	5th, 18th, etc.	13th, 26th, etc.	8th, 21st, etc.	3rd, 16th, etc.	11th, 24th, etc.	6th, 19th, etc.
	24	28	29	24	27	34	40	13	16	1	1	4	26
	14	21	18	19	16	37	22	21	24	20	14	30	22
	28	16	14	20	18	17	29	19	21	22	21	10	27
	18	16	19	19	27	30	27	27	29	19	10	17	12
Total	84	81	80	82	88	118	118	80	90	62	46	61	87
Second illustration													
	22	36	14	10	6	10	13	8	34	14	29	23	45
	20	18	3	6	15	1	6	13	22	30	49	29	29
	25	19	3	16	9	12	22	30	29	28	32	18	25
	7	32	28	14	20	29	9	10	11	13	16	30	23
Total	74	105	48	46	50	52	50	61	96	85	126	100	122

Or inspection having suggested the 2/5 pattern, in a trial such as in Table 13.

TABLE 13. *Lengths of internodes arranged in five orthostichies, the number appropriate to the 2/5 pattern, showing plus and minus sides*

	1st, 6th, etc.	4th, 9th, etc.	2nd, 7th, etc.	5th, 10th, etc.	3rd, 8th, etc.
	52	34	12	8	25
	46	35	16	5	27
	35	29	14	17	23
	26	22	14	18	28
	30	21	18	15	22
Total	189	141	74	63	125

Though in general tabulations such as these are not more than exploratory, they readily show, as these do, that contrasts may be rather sharp; and this altogether without the anatomy of the stem showing any bilaterality.

It is pertinent here to indicate that when there is a suppression, the internode apparently disappears along with the emergence. Stem no. 47 had three suppressions, one between *M* and *N* which were 27 mm. apart, one between *N* and *O* which were 1 mm. apart, and one between *O* and *P* which were 40 mm. apart. Stem 44 had fourteen suppressions and stem 50 had eight; or the three stems twenty-five in all. I do not give the individual lengths of the internodes, but their average which was 21 mm.; by it, though theoretically doubled, they had but the average length of single internodes. This disappearance of internode along with emergence is in line with the belief that the emergence in some way can determine the length of the internode. However, more data would be welcome.

20. BRANCHING

It is obvious that the buds of *Tamus* may be classed as of four kinds: (i) the underground perennial bud, sessile on the tuber; (ii) the buds of scale-leaves *A* and *B* which are nearly always underground; (iii) buds in the axils of scale-leaves and assimilating leaves up to the horizon where fertility begins, and (iv) buds that are indued with fertility. The last are distinguished by an almost invariable great reduction in the growth of the foliar emergences (bracts or prophylls) that they bear and by escaping apical dominance. Of them I have little to say. The perennial underground bud is a specialized bud and, by its lasting, quite apart from the rest. The rest are of two kinds, those underground whence stems may issue as large as from the perennial bud, and those from axils above ground whence, if stems issue, they are much more slender. The reason for this difference in performance is not evident. In the climate of England the underground buds are called on with great frequency to replace frost-injured main stems; but the above-ground are almost always, as regards replacing lost parts, just superfluities. I give here, as Fig. 51, an illustration of underground replacements.

The year 1944 was unusual in the severity of a frost on 8 May. The base of the stem figured here (Fig. 51) was taken from the ground in the summer of that year; it grew under a steeply embanked hedge and had ascended within the earth. Its history is patent. About the end of 1943 or very early in 1944 a cold spell had injured the apex, checking it at the horizon of scale-leaf *B* so that the senior bud in the axil of scale-leaf *A* escaped from apical dominance and grew; but the leader was only checked and resumed growth, extending its internode no. 3 with the internode 2_a from the scale-leaf *A* alongside. These two internodes manifestly kept pace. Parenthetically it may be remarked that the injury to the main stem appears to have prevented the crook, then at *B*, from straightening out by orthotropy. In May 1944 the severe frost, that has been named, killed both stems where they had reached the surface; after which both made good, the one with 3_x and the other with 4_x. These stems were not of less diameter than the parent would have been. Such is the way of underground replacements.

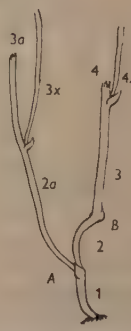


Fig. 51. Base of a stem twice injured by frost in its growth and branched in replacement, × ½. See text.

Before passing on, attention is drawn to the manner in which internodes increase in diameter, as figured, from the base upwards. We have seen the same phenomenon in the seedling (see Fig. 3 on p. 319), and we see the same in main stems but somewhat obscured by the thickening of the cortex; but Table 9 (on p. 364) shows that this thickening may be recognized in the stele under the thickened cortex; and stems are in general thinner, cortex included, for a few millimetres about the line of decay. It is a character got and kept in the process of strengthening.

If a stem be decapitated later than the time of frost injury, that is, after it has made a little growth above ground, aerial buds take up the business of replacing the loss, with this difference, that several will volunteer. The branches that they make are invariably slender. Is it to the diffusion of response over several axils that we should look for an explanation of the difference in their inability to equal the growth of underground buds? Stimulation comes to the underground buds when buds are few: for instance, when the stem of Fig. 5 was injured at scale-leaf *B* there was but one option, namely the oldest bud of the axil of scale-leaf *A*, for the junior buds of scale-leaf *A* were under the local dominance of the senior.

Of aerial branches I have found as many as twenty-three on a wild plant that had somehow lost its apex; and I have induced as many as fourteen to appear experimentally on a plant in my garden. I measured the lengths of all the branches on the wild plant with twenty-three; end to end they made 5½ m., of growth, i.e. more than any main stem makes, but by reason of their slenderness did not expend more material; they carried a greater number of leaves though with smaller laminae than the parent does.

Apical dominance is not so long lasting as to be a factor holding in buds in summer and would seem to be spent well before the apex of the stem begins to die, but it is operative after inflorescences have laid down buds; and there is no reason for connecting the liberation of buds to become inflorescences with its cessation. The little branches, such as in Fig. 11E, grow without the destruction of the apex, grow perhaps, in consequence of slight interference with the apex. The ability of buds to grow seems to be lost so nearly at the time when apical dominance is lost that the natural death of the apex does not free buds to grow.

There is no loss of ability to grow merely because the horizon of fertility is approached; for the last axil before the first inflorescence can be caused to produce a vegetative branch which may be as long as any that aerial buds produce.

I have found the transition from the vegetative potential to fertility hesitant in two plants. In one, a male plant, after two axils had given rise to panicles, the next two axils produced vegetative branches and the axils, after these four, produced panicles in an uninterrupted series. In the other, a female plant, there was a vegetative branch from the 41st node, followed by inflorescences from the 42nd and 43rd; then a vegetative branch 44 cm. long from the 44th, followed by inflorescences from the 45th to 57th at which the stem had been cut through. As both these abnormal stems were on wild plants their history is not known.

It happens, but is abnormal, that small cordate leaves appear on the lowest panicles. Normal bracts are not cordate, and they are not enlarged at all by the late basipetal wave of growth which enlarges the lobes of the assimilating leaves. An arrest blocking out this wave is part of the manner of shaping bracts and scale-leaves.

Every vegetative branch becomes the carrier of lateral fertile buds if it has length enough, but the ability to carry them is very much less in all aerial branches than on the parent stem.

In 1944, in preparation for experiments that I had planned, I transplanted into my garden parts of a large tuber, each part of 0·5–1 kg. The plant was female. I gave them a year in which to get established. In the spring of 1946 I decapitated the stems, and in September I examined the consequences. Also I included in the experiments a male plant grown from seed and five to six years old. Table 14 is from the male plant. It shows each branch to hold fewer bundles than the parent at the horizon of its origin, and the dimensions of the lowest leaf on each to be less than those of the axillant leaf.

TABLE 14. *Parent axis and branches compared in number of bundles and size of laminae*

	Bundles (common-cauline)		Lamina (length × breadth, and surface)			
Axil letter	In stem just below axil	In branch just above axil	of axillant leaf		of first leaf of branch	
L	10–8	6–5	71 × 83	34 cm.^{2}	63 × 55	21 cm.^{2}
K	10–8	5–5	68 × 75	30	65 × 51	17
J	11–8	7–6	75 × 78	31	61 × 46	15
H	11–9	6–5	64 × 68	24	44 × 34	7
G	9–8	7–6	56 × 64	19	46 × 36	9
F	9–8	6–5	66 × 67	17	43 × 30	6
E	10–7	7–5	59 × 59	18	38 × 26	5
D	9–8	7–6	60 × 62	17	40 × 26	5

The divergence of the lowest leaves of the branches was in the neighbourhood of 2/5 and that of the parent stem was 3/8.

The basipetal wave of growth which puts the final broadening to the lamina of an assimilating leaf is relatively weak in the laminae on branches with the consequence that the ratio of breadth to length is less in these than on the parent stem, as Table 14 indicates.

The male plant carried 7·7 m. of branches—i.e. a considerably greater length than any single parent stem can make. It was in its first flowering. The branch from *C* had its first flowers at its 13th node; the others successively at the 7th, 7th, 6th, 4th, 4th, 3rd, 3rd and 3rd.

A decapitated stem from one of the female plants gave origin to a short sterile branch from the axil of a lower scale-leaf, followed at the next node by a longer branch which began flowering at its 17th node and then by one from the next node which flowered from its 6th node forward. A second decapitated stem produced a branch below ground which flowered at its 30th node; immediately above ground were two short branches which did not flower, then four branches which flowered respectively and in this order—from their 22nd, 16th, 14th and 12th nodes. These data illustrate the extension of the zonation into the branches.

The stems of numbered plants of this experiment, 74–79, all female and of common origin by division of the tuber, were measured, and their lengths were as in Table 15.

Table 15. *Lengths in millimetres of all the uninjured branches of stems* 74–79 *followed by the number of internodes* (*this in brackets*)

Axil letter	Stem 78	Stem 75	Stem 74	Stem 77	Stem 76	Stem 79
T	—	—	—	581 (13)	—	—
S	—	—	—	201 (6)	—	—
R	—	—	—	84 (3)	728 (21)	—
Q	—	—	—	411 (9)	1176 (27)	—
P	—	—	1832 (34)	993 (13)	689 (16)	—
O	—	—	1693 (30)	246 (7)	1297 (26)	—
N	—	—	1809 (35)	388 (10)	1161 (31)	—
M	—	—	1543 (26)	Broken	1201 (27)	—
L	—	—	1802 (30)	34 (3)	1254 (31)	457 (6)
K	—	—	Broken	19 (2)	1061 (27)	918 (13)
J	—	—	1440 (28)	19 (3)	Broken	976 (16)
H	—	—	1023 (25)	12 (3)	717 (21)	908 (14)
G	—	140 (7)	409 (15)	27 (5)	711 (16)	717 (14)
F	—	345 (10)	265 (15)	—	Broken	837 (17)
E	—	30 (2)	Broken	—	655 (20)	726 (15)
D	34 (4)	323 (12)	2402 (56)	—	131 (7)	706 (16)
C	409 (15)	317 (9)	—	—	—	—
B	175 (9)	74 (6)	—	—	—	—

It is of interest that decapitation led to the release of buds in an unbroken succession of axils as showing that a zone of the stem had been completely in the condition for response. In illustration of this zonal condition, one may note that in stem 77 the axils *B* to *F* did not respond, nor in stems 76 and 79 did the axils of *B* and *C*, evidently because the buds below *G* in 77 and below *D* in 76 and 79 had lost enough of their power of immediate response to cause liberation from apical dominance to be without effect; but here we run into an unsolved difficulty—where there are three axillary buds in column of different priorities in an axil, do all lose alike their power to take on growth at the disappearance of apical dominance?

It is further to be noted that intensity of response showed zonation, so that on 76, for instance, there were successive branches of relatively little elongation; and on stem 77 which did not produce branches below *G*, the branches from *G* to *L* were all small, and there were longer branches higher up the stem among which there was a maximum responsiveness at *P*. The zonation of responsiveness can be read in the performance of other stems.

The stems differed among themselves considerably in the vigour of their branches, for which no reason was apparent.

It is a rule that the longer the branch, the longer its internodes:

Those of 2–5 internodes had an average length of 10·24 mm.
„ 6–10 „ „ 28·10 „
„ 11–20 „ „ 35·67 „
„ 21–30 „ „ 47·50 „
„ 31–40 „ „ 45·23 „

Also it would seem that, under the conditions in which my plants were grown, the longer aerial branches attain one-tenth of the length of the main stem.

There are plus and minus sides in a branch; and the divergence at the base, being in the nature of 2/5, places the 3rd, 5th and 8th emergences on the plus side (see the graph, lower inset to Fig. 47). I do not need to give the precise averages. As very short branches have their 1st internode longer than the others on account of the onset of exhaustion, the inclusion of short with long branches in obtaining averages depresses the average for the later internodes against the first; but that does not interfere with the evidence that the average gives of the existence of plus and minus sides. When I took a group of branches, eliminating all the shorter, the 5th internode was found to have the greatest length, as shown in Table 16 and in the lower inset to Fig. 47. The curve of this inset is reminiscent of the curve of the spring push, and that is why I have brought the two insets into apposition. The reader will note that I have brought the 5th internode of the average of branches under the 4th internode of the average of the spring push and may ask why I have done so. The answer is because there is no internode in the main stem under the calyptra, the 5th internode of the branches corresponds to the 4th of the main stem.

TABLE 16. *The lengths in millimetres of the first ten internodes of eleven branches produced by the three stems from one hedgerow tuber (no. 42, etc.), the longest branches only*

	Internode no.									
	1	2	3	4	5	6	7	8	9	10
	1	30	43	37	112	45	53	93	8	80
	9	41	46	46	150	19	72	56	25	41
	5	23	36	39	76	2	61	39	10	48
	18	38	62	50	97	2	62	42	2	31
	4	29	0	79	104	59	18	52	18	28
	2	10	23	34	73	27	42	44	50	37
	10	26	31	40	79	7	11	22	8	2
	10	38	42	50	46	7	41	25	0	38
	15	13	40	45	75	4	55	46	1	60
	13	18	19	10	49	15	0	37	5	16
	8	30	37	20	88	2	40	33	11	29
Averages	9	27	34	41	86	16	41	45	15	37

We get a welcome shaft of light on the nature of the spring push from these experimental branches. As a preliminary it is to be recalled that they are long branches, and to be mentioned that they have been used because there should be no effect of exhaustion in data from beyond the 10th internode, any more than in data of the horizon of the spring push on the main stem which of course is a branch itself. Thus is the graph of the lower inset, namely a curve derived from the averages given in the last line of Table 16, rightly comparable with one of average lengths of internodes at the base of main stems. We learn from such a comparison to expect a peak where the spring push is—though produced without the aid of the spring push, because the strengthening of the axis leads up to a 5th internode and the plus and minus influences intensify that as a peak, the ganglion of the internode being a plus ganglion by the divergence. What the spring push actually does is to exaggerate the height of its peak. The emergence of the stem into light and air must entail a jolt to the physiological balance of the stem such as would hasten some process which sends unusual quantities of a growth stimulant into the stem and so it would happen that the internode ripest to respond, coincidentally the 4th of the stem (5th if we credit a zero internode to the calyptra), elongates to make the peak itself. Three factors in this contribute: strengthening, the plus side, and the condition of being ripest; and what it is that the excesses in Table 11 in standard deviation for the waning of the spring push over the summer growth indicate is the factor of being ripe to respond. The reader will now share my regret that work with moving averages by groups as large as thirteen, places outside the calculations the first seven internodes wherein is the actual peak.

21. Initiation of new heads

I had hoped that an examination of the process by which new heads are produced on headless tubers would supply information bearing on first divergences; but I have obtained little by this means. Serial sections of wens in process of becoming organized at the apex showed, first, rupture of the cork of the tuber by the outgrowth which immediately gave origin to new phellogen, only to rupture the thin layer of cork then formed. The wen enlarged into the form of a mamma, i.e. it broadened at the base, and then growth slackened just behind the apex leading to the production of a vallum; and within the vallum which remained open on one side, the organs indicated in Fig. 52 appeared in that particular mamma. Of phyllotactic pattern there was none; roughly the divergences in the case figured followed each other thus: 90, 144, 80, 220 and 228°. *A* and *B* showed axillary buds. The vascular bundles at different horizons were 11 and 12 in number.

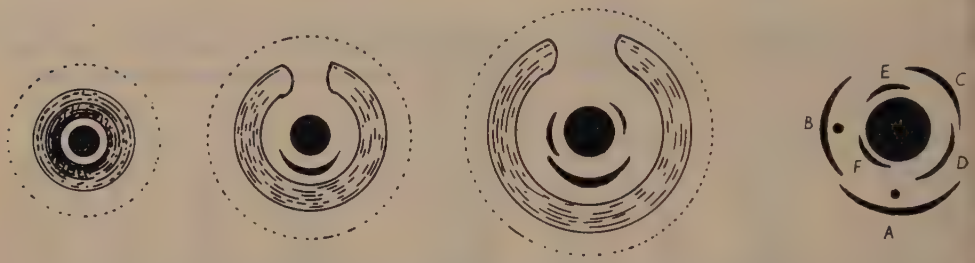


Fig. 52. The formation of a new head: three observed stages and a diagram of a more advanced fourth stage. Explanation in the text.

This brief notice should be a starting-point for more extensive examinations, with in mind the possibility of suppressions.

22. On the ancestry of *Tamus*

Of the two species that compose the genus *Tamus* neither as yet seems to me to be more ancestral than the other; but I have been unable to examine *T. edulis* alive. It occurs near the sea-coasts of Madeira, Gran Canaria, Teneriffe and Hierro; and it is encouraged by a little cultivation for its tuber, although this is said to require ten to twelve hours' cooking. The presence of this endemic just off a route by which an ancestral *Tamus* could enter Europe from Africa is evidence of phytogeographic importance. *T. communis* is rather widespread in the Moroccan Atlas and near the coast, is in the mountains of Algeria and near the coast, in Tunisia, and in Cyrenaica in certain valleys. Its limits southwards are beyond all doubt determined by water: but pluvial periods in Africa north of the equator, for the occurrence of which geologists have evidence, had possibly allowed *Tamus* or its immediate ancestry an extension southward far beyond its present limits, and it would be unreasonable to discount the evidence of close kinship in the similarities between *Tamus* and the South African *Dioscorea* (*Testudinaria*) *elephantipes*, on the ground that their homes are now so far apart. The genus *Dioscorea* is widespread, being pan-tropic with extensions into temperate climates, and is not less well represented in Africa than elsewhere. *Tamus* obviously evolved by the conversion of the capsule of *Dioscorea*—I believe of an African *Dioscorea*—into a berry (there is no other difference) by the fleshiness of the ovary-wall persisting, perhaps increasing, until so near seed-ripening that distribution by wind was interfered with and distribution by birds adopted.

Otherwise, the way of life, the tropophytic habit, storing organs underground, twining stems and even the precise number of six seeds in the ovary were accepted unaltered.

Tamus communis is a good time-keeper in England. Autumn flowering is recorded in one County Flora (Leicestershire) and I have myself once found male flowers in early October; this was in Devon and the plant had suffered injury: otherwise it flowers reliably in June with a slight overlap into May and July. Its annual cycle is dated from the end of August,[1] at which time it begins to cut off the living foliage and the ripe to unripe berries of the year by the self-pruning that I have described (p. 324). Then a new growth is initiated in the face of winter. In England, France and Switzerland moisture enough reaches it in winter from the Atlantic to allow its stems to elongate slowly in the soil; and they come above ground after mid-March. But in Gibraltar, in favoured localities in Algeria, and in Palestine it is so much earlier as to flower in March. The fruits turn red three to four months later; and the period brings an end to the year's cycle, an end which in these southern countries is not in the face of winter, but of the fierce heat of the end of summer. It would be by avoiding desiccation at this time that it survived as a tropophyte, and the inherited quality happened in its case to enable it to survive winter cold further north. Europe, as Raunkiaer has pointed out (*The Life-forms of Plants* (1934), p. 102) is a veritable haven for plants of its way of life; and it is not difficult to believe in it having drifted into Europe. I think that this was so.

Von Mohl, on his transfer in 1835 to Tübingen, found that his predecessor had received seed of *Dioscorea elephantipes* from South Africa and had raised plants, then some three years old. He began to study them and sowed more of the seed, but this seed was dead. He was consequently debarred from examining germination. To help himself out he turned to *Tamus communis*, nothing being more natural, for the *Dioscorea* was at the time thought to be a *Tamus*. What he had to record, including a correction of Dutrochet (in *Nouv. Ann. du Mus. d'Hist. Nat.* (1835), 4, 172), he published in his *Vermischte Schriften* (1846, pp. 186–95). The gap which he was forced to leave was bridged by Miss Sparshott (Mrs Warren) whose paper (in *J. Linn. Soc. Bot.* **49**, 1935, pp. 593–610) is of great value. Her material was not from the true *Dioscorea elephantipes*, but from the closely akin species which Marloth segregated under the name *Testudinaria glauca*. When this plant is transferred to the genus *Dioscorea* it cannot be called '*D. glauca* (Marloth)' as the epithet is occupied already; and I call it **Dioscorea hemicrypta**. The characters which Miss Sparshott found in it, that are shared with *Tamus communis* are: (i) the tuber becomes visible laterally on the stem of the newly germinated seedling; (ii) the first and only expanded leaf of the first season has dominance over the next and arrested leaf; and (iii) it is characterized by a long petiole; (iv) there is a preparedness in the second leaf to replace the first if the latter be destroyed; (v) a brood-chamber is formed by the bases of these two leaves; (vi) abundant colleters appear on the first leaf; (vii) a single vascular strand connecting cotyledon and radicle is the first vascular tissue; (viii) a sympodial building up of the stem-bud follows; the bud is sessile on the tuber; (ix, x) the years after the first bring a gradual increase in the number of internodes in the stem, with the stem's arrest abrupt after the node of a full-grown leaf; and (xi) the first scale-leaves are characterized by a breadth beyond that in others. The similarities are impressive.

Miss Sparshott found multiple buds in the axils. They, however, are widespread in Dioscoreaceae.

The upward increase in circumference of the stem is not shared, nor the duration of after-ripening, for her seed took only two to three weeks to germinate.

The tuber of *Dioscorea elephantipes*, in the course of growing, becomes blunt, then somewhat concave at the lower end, which enables the origin of the platelike tuber of *D. sylvatica* Eklon, to be understood. The first leaf is at about 180° to the cotyledon across the cauline apex; and the leaves are all alternate. Beyond this the materials fo comparing it with *Tamus* have yet to be collected.

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[1] If the head of a tuber be extensively damaged during the summer, the date of outgrowing may be advanced; and this suggests how secondary is the part that temperature plays.

Little pertinent enough for quotation here is known of other African Dioscoreas excep that the stems of several Madagascan species are ridged like that of *Tamus* and hav soft prickles and also that the walls of the ripening capsule of one species are peculiarl fleshy.

23. Conclusion

Because this paper is intended to lead up to comparisons in behaviour of *Tamus* wit various species of *Dioscorea*, the most appropriate way of bringing it to a conclusion lie in enumerating the characters revealed that have to be sought in turn in allied plants.

(i) The *position* of the *line of self-pruning* (Fig. 7A on p. 324) is a major epigeneti feature: it is immediately above the basal node of the annual stem so that the prunin *cuts off every part that is dispensable.* The time of its appearance would seem to hav become part of the plant's behaviour as a protection against drought coming in associatio with heat. Equally this adaptation of resting under the soil is protective against injur by cold and again against injury by animals that seek tubers for food. By the protectio given against cold, *Tamus* would seem to have been enabled to advance northwards i Europe (p. 377) to limits apparently determined by frost-penetration into the soil. Th species has methods of sinking into the soil, operative in the seed (p. 314), in the seedlin (p. 321) and in the mature plant (p. 321), by which exposure to injury may be increasingl avoided.

(ii) The specialization of the *hypocotyl* whereby it gives origin to the *tuber*, is very great Its growth begins in an interplay between polarity and an intense positive geotropis (p. 316). In the end the tuber takes over all the business of the plant with the soil. Ther is nothing unusual in the lower end of the stem of a monocotyledon doing this; but th accompaniment of secondary thickening in its tuber, it being a monocotyledon, is mos unusual; and the sharing of the character with the section *Testudinaria* of the genu *Dioscorea* is a compelling argument for regarding *Tamus* as of origin where *Testudinari* originated, i.e. in Africa (p. 376).

A greatly widened knowledge of germination in the Dioscoreaceae is desirable an particularly of the behaviour of the hypocotyl.

(iii) The geotropism seen in the hypocotyl of the newly germinated seedling of *Tamu* is never lost (p. 316); nor is the polarity which is perpetuated in zonal production b tubers of adventitious roots and in regeneration of new cauline heads (p. 322).

(iv) The downward elongation of the tuber of *Tamus* is never arrested; but the downward elongation of the tubers of *Dioscorea* (*Testudinaria*) *elephantipes* and *D.* (*T.*) *hemicrypta* is arrested as the plants mature, and that of *D.* (*T.*) *sylvatica* is arrested so earl that its tuber makes a flat plate. The condition of *Tamus* seems the more primitive.

(v) *Secondary thickening* in the tuber of *Tamus* is by a continuous *Growth zone* wit a polar control of its intensity leading to little enlargement above. The formation o outgrowths in and about the buds at the head of the tuber is not exactly the work of th growth zone, but seems to be a response to stimulation by the buds (p. 320). It is no yet certain how the growths compare with upward growths in *D. alata* at the top o the tuber.

(vi) New axes in the *buds in the head of the tuber* are for the most part formed befor a necessity for them is apparent; but their growth is immediately arrested. They ma remain long resting in a very small state until they are committed to grow.

(vii) Each axis of a bud, immediately it is initiated, produces one foliar organ which has preference of growth against the axis and envelops it. So to behave is characteristi of the genus *Dioscorea* as well as *Tamus*; and this protecting and highly specialize organ needs a name. It is conveniently termed the *calyptra* on account of its shap (pp. 318, 324).

(viii) The minuteness of the axis is accessory to that enveloping whereby the *calyptra becomes amplexicaul* (p. 318). The scale-leaf which follows next after the calyptra, here called scale-leaf *A*, approaches an amplexicaul condition; and the fact may be accepted that it is enabled because the axis is still very small when it appears (p. 325). The cotyledon, earlier, had shown itself amplexicaul (p. 313) and obviously was assisted in becoming so by the smallness of the arrested cauline end that it embraces.

(ix) When this small bud is committed to grow, it does not strengthen itself before it begins to elongate, but it *elongates while it strengthens*; and the base of the stem does not attain then or at any time the circumference that the stem attains upwards, the maximum circumference being ten to fifteen nodes from the base (p. 330). Among grasses *Zea mays*, among Palmae and Pandanaceae several species, among Cactaceae many species, and among Bombacaceae such genera as *Cavanillesia*, have stems or trunks that *increase in circumference upwards* from the base; but no climbers other than *Tamus* are known to do so. *T. communis* from its maximum circumference upwards suspends its weight on the shrubs that it victimizes for support (p. 314), and is erect and self-lifting below; and in this part a lighter construction serves because the upper weight will be taken away as it appears.

(x) The *scale-leaf A*, though specialized, is not so specialized as to need a name (p. 325). Its nearly amplexicaul base enables five or seven vascular bundles to pass between it and the stem. But the next scale-leaf after it and all the other scale-leaves and assimilating leaves along the stem receive three bundles only (p. 337). It may be assumed that when scale-leaf *B* is formed the axis has strengthened to a size that does not permit amplexicauly to be approached or the bundles to be more than three.

(xi) The *vegetative line of the axil* diminishes along the stem from the base of the stem to its distal end (p. 353); and this it does irrespective of the increase (and subsequent decrease) of the circumference.

(xii) Under each emergence is a *vascular ganglion* whence the leaf-trace descends (p. 337). As this ganglion and the leaf-trace are in intimate relationship to the vegetative line of the axil, the ganglion and leaf-trace share with the vegetative line the property of diminishing in size from the base of the stem to its distal end (p. 353).

(xiii) The *angle of leaf-divergence*, like the width of the vegetative line, diminishes from the base of the stem to the distal end (p. 361); basally it is 180° and distally in the neighbourhood of 120°, i.e. it passes from an angle that gives distichy to one that gives tristichy. This it does irrespective of the increase (and subsequent decrease) of the circumference. It has long been a matter of comment (see Hofmeister's *Handb. d. allgem. Morphologie* (1867), **1**, 461, 488) that there are monocotyledonous plants wherein the disposition of the leaves is inconstant between distichy and tristichy. *Tamus* is to be added to them; and, having gradations that are very much extended, it is a far better subject for study than they.

(xiv) If it be right, and assuredly it is right, that divergence depends on the size of the area each successive emergence demands in relation to the area that the apex has to offer, then if there be a measure of constancy in the areas demanded, diminishing divergence indicates increasing available area in the apex. In *Tamus* scale-leaf *A* appears at 180° to the calyptra (p. 325), i.e. at the maximum divergence; and the divergence is indicative of the minimum area being available and that this minimum area is occupied by the scale-leaf at its initiation when the axis has strengthened enough to add one to the calyptra. With further strengthening comes the production of emergences at lesser angles of divergence, and distichy begins to pass over to tristichy, which it must do through a pentastichy dependent on two turns of the spiral, the divergence angle of which is 144°. This angle is reached at about the 5th–8th nodes (p. 348). The *narrowing of the divergence* gives a measure of the strengthening and, like the passing away of amplexicauly, is a demonstration of the strengthening.

(xv) The *maximum circumference* of the stem is to be sought a little beyond the 10th node, and may be taken for the limit of the strengthening effort as regards the stem.

Then follows the maintenance of strength which will pass into loss of strength. Elongation is not identical with strengthening.

(xvi) The *genetic spiral* is brought into being by the plant determining which margin of an existing foliar organ the next organ shall approach when the angle of divergence falls from 180° (p. 339).

(xvii) A ganglion is less likely to be a replica of that which immediately precedes it in the basal part of the stem than at any higher horizon. This fact is connected with the circumstance that *the ganglion* is *reshaped* later than its initiation: in fact two rhythms have to be kept in mind; one is that of the calling of the ganglion into existence and the other of the consequence of later ganglia obtaining anchorage in it. The ganglia record both rhythms; and, where they are few in number by reason of leisurely initiation because the axis is too weak to initiate freely, they carry the record of a crowding of anchoring bundles towards them. They must remain long in one physical condition for slowly formed ganglia higher in the stem to be able to anchor.

(xviii) The number of bundles in a leaf-trace is invariably five, and the width of leaf-traces diminishes from the base to the distal end of a stem. As the circumference of a stem increases upwards to a maximum and then diminishes, there is an interaction between these which carries *the horizon of the greatest number of bundles* to a position on the distal side of the horizon of greatest circumference. As the divergence also diminishes from the base to the distal end, there is a gradual removal of bundles from the interspaces between unbroken leaf-traces. Of characters in the stem those closest in origin to foliar development appear most standardized.

(xix) Not only do the *foliar emergences* appear standardized, but they *acquire an autochthony* by which they complete themselves, that may be operative in positions of competition against the axis for growing material. By this autochthony the cotyledon pushes aside and dwarfs the cauline apex (p. 313) and the first assimilating leaf grows with the axis arrested at the side of it in the first summer; and again, the process is repeated in the second summer; furthermore, the stem ends its foliage every year by a leaf that is fully formed, while it, the axis, is dying to the node at which that leaf is (p. 341).

(xx) The *previsual history of the apex* is to be understood in this manner: morphogenetic fields are initiated rhythmically and become self-centred, withdrawing from a neutral belt of cells between them. Provided the rhythm and the enlarging growth remain constant, these belts keep approximate equality of width about the field; but the polarity of the axis soon interferes; and then they become unlike in directions determined by the polarity. The belts, for instance, will become internodal in the direction of the polarity. Being in need of a word for the belt in the direction that cuts transversely across the polarity, I have adopted *interspace* (p. 354). Internode and interspace have quite unlike growth after the entrance of polarity, whereon the vascular bundles taking their course under polar direction appear threading through the interspaces, linking each new field to some old field according to convenience within the axis.

(xxi) *Excess growth of circumference* goes to enlarge interspaces (p. 356). Interspaces can be measured by the number of bundles which thread them through, as the relatively even spacing of the bundles in the stem makes this possible. Interspaces must have attained their full proportion of width at the time when provascular strands appear in them as heralds of the vascular bundles.

(xxii) From the circumstance that the *angles of divergence* dwindle from the base while the circumference is increasing and continue to dwindle afterwards, while the circumference is decreasing, they have no direct connexion, as have the interspaces, with the changes in circumference. This is what would be expected, the angles having been determined in an activity still earlier than that which widens the interspaces.

(xxiii) With interspaces distributed evenly around the stem, divergence angles are not altered whatever the width of the interspaces; and they have never yet been found unevenly distributed. To this the predominance of three pairings of bundles (p. 365) is conformable, three being suited to a tristichous disposition of leaves.

(xxiv) This *pairing of common bundles* arises when an interspace departs at a node from the width that regularity would maintain by as much or it may be a little less than the width of one bundle. Then a descending bundle misses the ganglion and runs further, parallel to the marginal bundle of the leaf-trace. Should the descending bundle be of the kind called common and therefore of the same ring of bundles as the marginal bundle of a leaf-trace, pairing results. Should the descending bundle be of the kind called cauline, there is an increase by one bundle in the ring, without the development of pairing. For a description of common and cauline bundles, see p. 333.

(xxv) *Cauline bundles are double bundles*; and sometimes the two parts separate at a node, one part adsorbed, the other passing further.

(xxvi) *No bundle travels further* than through eight internodes. This is attributed (p. 358) to the necessity of the ganglion whence the bundle descends and the ganglion in which it anchors being in a kind of *metabolic* harmony. The limitation has the geometric consequence of preventing the occurrence of three common bundles running side by side (p. 357) and rules out as impossible the development of various otherwise geometrically possible phyllotactic patterns.

(xxvii) It appears that a maximal increase in size of stem may introduce an arrangement which is, as it were, a falling apart of the mesh of bundles and *provocative of fasciation* (p. 358). It appears also that a decrease in size may produce such complications that the system breaks down from want of room; then the cauline bundles fail to appear before the common (p. 364). *Limiting factors* in increase or decrease of size would thus be imposed on the stem.

(xxviii) *Suppression of emergences* is frequent (p. 346); and a cause would appear to lie in phyllotactic alterations which lead to one emergence interfering with another. A suppression leads to the genetic spiral appearing reversed (p. 339). Statements in botanical literature of reversed genetic spirals are due for revision.

(xxix) The linking of the ganglia together is certainly the end of one *period in the ontogeny* of the stem: the next establishes autochthony in the foliar organs that the stem has originated.

(xxx) There are *buds in every axil*—at least one; and in the lower there are three in column, the senior uppermost. All buds are of vegetative potentiality up to a certain horizon, which is lower in the male than in the female (p. 330); above this horizon the buds have a reproductive potentiality. All buds with vegetative potentiality after formation are arrested by *apical dominance*; but the reproductive buds are not. Apical dominance is a power of like to arrest like: it extends through all the vegetative buds, even so that the senior of multiple buds in an axil exercises it over the others: it is a power of the larger of a kind over the lesser. It cannot happen that the death of the apex which is almost invariable (p. 372) liberates the lateral buds, as these buds have lost their initiative more or less before this time. But the bud in the axil of the calyptra is in a different category, and does not lose its initiative with the others.

(xxxi) *Buds* liberated to grow *from the axils underground* grow into the equivalent of the parent; but aerial buds produce weaker branches (p. 373).

(xxxii) Buds liberated to grow stimulate a *responsive growth* in the stem (p. 327), and, it would seem, also in the head of a tuber (p. 319).

(xxxiii) It is difficult to collect a sufficiency of data of leaf-suppression to show exactly that the internode below a suppression is suppressed; but such data as have been obtained suggest that it is suppressed: and this intimacy of internode and emergence would be expected.

(xxxiv) A new *stem ascends in the soil* bent into a crook whereby the more tender parts are not pushed upward but are drawn upwards under a knuckle that takes the rub with the soil. It is clear that an *auxin from the scale-leaves* stimulates the growth that bends the stem into the crook, and that this auxin acts on growth over a restricted stage. Later, orthotropy straightens the stem.

(xxxv) A hormone, doubtless identical, bends petioles in the same way under particular conditions (p. 328) and petioles of expanding assimilatory leaves on stems at large (p. 328).

(xxxvi) The occasion of the *emergence of the stem from the soil* in spring gives to the activity a powerful jolt which leads a zone of internodes that happen to be in the appropriate condition of receptivity to a noteworthy exaggeration of the elongation that would have been theirs proportionately (pp. 365 and 375) and the exaggeration is biologically important to the plant as its *spring push* (p. 313).

(xxxvii) The emergence of the stem from the soil is the first occasion on which a stem can respond to *heliotropic stimuli*, and the stem turns horizontal in the surface of the soil (p. 329) by a flexure at a node. The position of this flexure, being with the convex side at the base of a scale-leaf, indicates that the scale-leaf plays a part in producing it. It is a response that advantageously deploys stems when several arise on one tuber.

The *nodal flexures* of weak branches (p. 330) and, it may be added here, of male flowering spikes in Dioscoreas such as *Dioscorea alata* Linn. invite comparison.

(xxxviii) The *stem is bifacial* in the very curious way described in section 19 (p. 365). When the foliar emergence is on a plus side, the internode below it elongates beyond the average; when it is on the other side, it does not reach the average. The plus side is the side of the calyptra and the minus side the side of scale-leaf A. As the calyptra has its back more or less towards the parent axis (see Fig. 4, p. 320) the stem is *plus adaxially* and *minus abaxially*. There is no evidence yet how the elongation is determined. It may be thought that the stimulation to grow comes from the foliar organs and acts on an axis differently receptive on the opposed sides. As that should lead to bending, as in the formation of the crook, the supposition leads to a further supposition, namely that there is such orthotropy as to spread the stimulus immediately to all sides of the stem.

(xxxix) *Branches* of whatever rank *are all bifacial* and this from base to apex.

My most grateful thanks are given to Prof. J. McLean Thompson for a very generous discussion with me of the problems that my study has raised, and for much help.

A Revision of the Genus *Otiophora* Zucc. (Rubiaceae). By Bernard Verdcourt

(With 5 Text-figures)

[Read 24 November 1949.]

Introduction

The genus *Otiophora* was founded by Zuccarini (1832) for a plant found by Bojer in Madagascar. This plant, *O. scabra*, is the type species of *Otiophora*. The genus remained monotypic for some fifty years, until Baker (1883) described a further species, *O. pauciflora*, also from Madagascar. Between these two dates another species, clearly belonging to this genus, was published under the name *Anthospermum calycophyllum* Sond. (1865). This, however, was not recognized as being a member of the genus until 1901, when K. Schumann incorrectly synonymized it with *Otiophora cupheoides* N. E. Brown (1884), from which species it is quite distinct. After 1880, numbers of new species were described and a list of those at present recognized by the writer follows:

Check list of species and varieties of *Otiophora*

1. *O. scabra* Zucc.
1*b*. var. *diffusa* Verdcourt, var.nov.
1*c*. var. *glabra* Verdcourt, var.nov.
2. *O. spirospicata* Good.
3. *O. calycophylla* (Sond.) K. Schum.
4. *O. inyangana* N. E. Brown.
4*b*. var. *parvifolia* Verdcourt, var.nov.
5. *O. cupheoides* N. E. Brown.
5*b*. var. *macrosiphon* Verdcourt, var.nov.
5*c*. var. *hirsuta* (Bär) Verdcourt, comb.nov.
6. *O. pycnoclada* K. Schum.
7. *O. hebe* Verdcourt, sp.nov.
8. *O. pycnostachys* K. Schum.
9. *O. caerulea* (Hiern) Bullock.
10. *O. multicaulis* Verdcourt, sp.nov.
11. *O. latifolia* Verdcourt, sp.nov.
11*b*. var. *villosa* Verdcourt, var.nov.
11*c*. var. *bamendensis* Verdcourt, var.nov.
12. *O. parviflora* Verdcourt, sp.nov.
12*b*. var. *stolzii* Verdcourt, var.nov.
12*c*. var. *iringensis* Verdcourt, var.nov.
13. *O. pauciflora* Baker.
13*b*. var. *ovata* Verdcourt, var.nov.
13*c*. var. *burttii* (Milne-Redhead) Verdcourt, comb.nov.
14. *Otiophora* sp.
15. *O. villicaulis* Mildb.

The remaining names which have been published in the literature have been treated as follows:

O. densiflora Bär = *O. cupheoides* var. *hirsuta* (Bär) Verdcourt.
O. caespitosa S. Moore = *O. pycnostachys* K. Schum.
O. pulchella K. Schum. = *O. caerulea* (Hiern) Bullock.
O. angolensis Good = *Otomeria angolensis* (Good) Verdcourt, comb.nov.[1]

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[1] **Otomeria angolensis** (Good) Verdcourt, comb.nov. *Otiophora angolensis* Good in *J. Bot., Lond.*, **64**, Suppl. 2, 40 (1926). The type of this species has been examined (*Gossweiler* 5797, Herb. B.M.),

ABBREVIATIONS

The letters in brackets after citations of sheets refer to the Herbaria from which sheets have actually been examined:

B. = Herbier du Jardin Botanique de l'État, Brussels.
B.M. = British Museum (Natural History), London.
K. = Royal Botanic Gardens, Kew.
P. = Muséum National d'Histoire Naturelle, Paris.
S. = Government Herbarium, Salisbury, Southern Rhodesia.
s.n. = sine numero.
V. = Herb. Musei Palat. Vindob.

GENERIC DIAGNOSIS OF *OTIOPHORA*

At the time of Bentham and Hooker's *Genera Plantarum* (1873) only one species of *Otiophora* had been described. The reference to 'species 3, Madagascarienses' at the end of their diagnosis is presumably an error. The concept of the genus has naturally widened considerably since 1873, and an emended diagnosis is given:

Herbs or suffrutices, annual or perennial. Erect, procumbent or straggling in habit. *Stems* solitary or caespitose from a ± woody rootstock, glabrous or hairy. *Stipules* small, connate with petiole, fimbriated into ± linear segments. *Leaves* very variable, usually small, 0·5–4 cm. long, membranous or coriaceous, round to linear, sessile or shortly petiolate, paired, in whorls of three, or pseudo-verticillate. *Flowers* small, hermaphrodite, not dimorphic, geminate, in long to short spikes, or in dense heads, or in a combination of both. Pedicels very short, often woody, persistent. *Calyx tube* ovoid to rectangular, glabrous or hairy, adnate to ovary. Calyx lobes 5, 1–3 much larger than the rest, foliaceous and resembling in shape and texture the leaves of the species concerned, or 1–2 foliaceous plus 1–2 foliaceous but smaller, remainder in each case reduced to minute teeth or bristles. Calyx persistent on fruit. *Buds* with limb abruptly expanded into an ovate or subcylindrical head and clearly distinct from the tube, or clavate and limb merging indistinctly into tube. *Corolla tube* extremely filiform, often thirty times as long as broad, but in those species where tube and limb of bud are merged, the tube is somewhat infundibuliform even when the flower is fully mature. Corolla tube 3–12 mm., usually glabrous but occasionally hairy in *O. pauciflora*. Throat of corolla glabrous except in *O. inyangana*, where it is densely hairy. Corolla lobes 4–5, ovate to narrowly lanceolate, from one-third to two-thirds the length of the tube, patent, valvate, glabrous or hairy externally, sometimes with very minute white scales adnate on both sides. *Stamens* 4–5, exserted for a distance nearly equal to length of corolla lobes. Filaments filiform, inserted at throat of corolla, usually glabrous, but in two species with hairs or hairy projections at the base. Anthers oval to oblong, affixed dorsally near their base or middle. *Style* glabrous, filiform, exserted for a distance equalling the length of corolla lobes (including stigma). Stigma bifid, lobes filiform, glabrous, 1–4 mm. long. Ovary bilocular. Ovules, one in each loculus, elongate to ovate, erect, attached to partition very close to base. *Capsule* ovate, subglobose or oblong, usually splitting into two mericarps one of which is crowned by the foliaceous lobe or lobes. Seeds black, granulate, subglobose, ovoid, or oblong, depressed ventrally, convex dorsally, sometimes slightly keeled mid-dorsally, and with a round, oval or linear fovea surrounding the hilum corresponding to the shape of the seed.—Species 13, Madagascar, Tropical and South Africa.

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and though extremely similar to *Otiophora* in general habit, the presence of numerous ovules, and of a corolla tube abruptly dilated just below the lobes shows that this species is a perfectly typical member of the genus *Otomeria*. The stamens are sessile in the dilated portion of the corolla tube and the stigmas are hairy.

Geographical distribution

The approximate distribution, so far as is known, is shown in Fig. 1. Two species occur in Madagascar, *O. scabra* and *O. pauciflora*, and all thirteen occur on the African mainland. Three species and two well-marked varieties occur as far south as, and are so far only recorded from, the Transvaal, viz., *O. cupheoides*, *O. calycophylla* and *O. hebe*. A variety of *O. latifolia* occurs at Bamenda in the Cameroons, and this is the recorded western limit of the genus. *O. pauciflora* var. *burttii* occurs in the Virunga mountains, both in the Belgian Congo and in Uganda, and *O. pycnostachys* is recorded from Lake Nabugabo near Masaka, Uganda. These records represent the northern limits of the genus so far as is known at present. *O. inyangana* is recorded only from eastern Southern Rhodesia, where it is common; *O. spirospicata* and *O. pycnoclada* are at present known only from individual localities in western Angola and southern Tanganyika respectively. The other species are distributed, some widely, in central Africa, as shown on the map.

Affinities of the genus

Otiophora belongs to the tribe Anthospermeae of the subfamily Coffeoideae. It is now widely recognized that the present classification of the Rubiaceae, based as it is on the number and position of the ovules, frequently cuts across natural relationships. *Otiophora* shows affinities with *Otomeria*, *Pentas* and *Pentanisia*, in addition to *Anthospermum* with which it is at present classified. It is, however, an extremely natural genus and does not merge gradually into any of the related genera. It is true that *Otiophora pauciflora* shows a striking resemblance to *Anthospermum herbaceum* Linn.f. in habit, and sterile material is difficult to separate. The latter is, however, clearly distinguished by its heterostylous and usually unisexual flowers, and by the fact that the fruits are not crowned by the persistent foliaceous calyx teeth as is always the case with *Otiophora*.

Subdivisions of the genus

There is a great diversity in habit amongst the various species of the genus, and though most of the species are recognizable at a glance by a combination of many characters, they nevertheless vary over a wide range. *O. scabra* varies considerably in habit, and often resembles many of the other species by being shrubby, or caespitose, or even straggling. The foliage of most of the species is particularly variable, but usually characteristic in a way which is difficult to describe. The foliage of *O. inyangana* is sometimes very similar to that of *O. cupheoides*; that of *O. scabra* sometimes resembles *O. pycnostachys*, and the leaves of *O. caerulea* vary from linear to elliptical. The flowers are rather constant in shape throughout the genus. The hairy appendages found at the base of the filaments in *O. spirospicata* might be thought sufficient to warrant the erection of a subgenus, but the same character is to be found to a less marked degree in *O. pycnostachys* which is not sufficiently close to *O. spirospicata* to form a well-marked group with it. The hairy throat of *O. inyangana* distinguishes it from all the other known species, but it closely resembles *O. cupheoides* in bud characters. These two species do in fact form a well-marked group distinguished by the shape of the buds. Occasionally, however, *O. inyangana* shows a slight variation in its buds and an approximation to this type of bud can be seen in *O. calycophylla*. *O. scabra* and *O. spirospicata* are linked by their long spicate inflorescence but not by other characters. The inflorescence in the other species varies widely and suggests that evolution has proceeded from a long spike to a dense head. It is considered that no groups in the genus are sufficiently well characterized to merit the erection of subgeneric divisions.

Relationships between the species

Some of these relationships have been mentioned in the preceding section, and others will be noted in the specific accounts. *O. scabra* is considered to be the most primitive species of the genus by virtue of its long spicate inflorescence and wide distribution

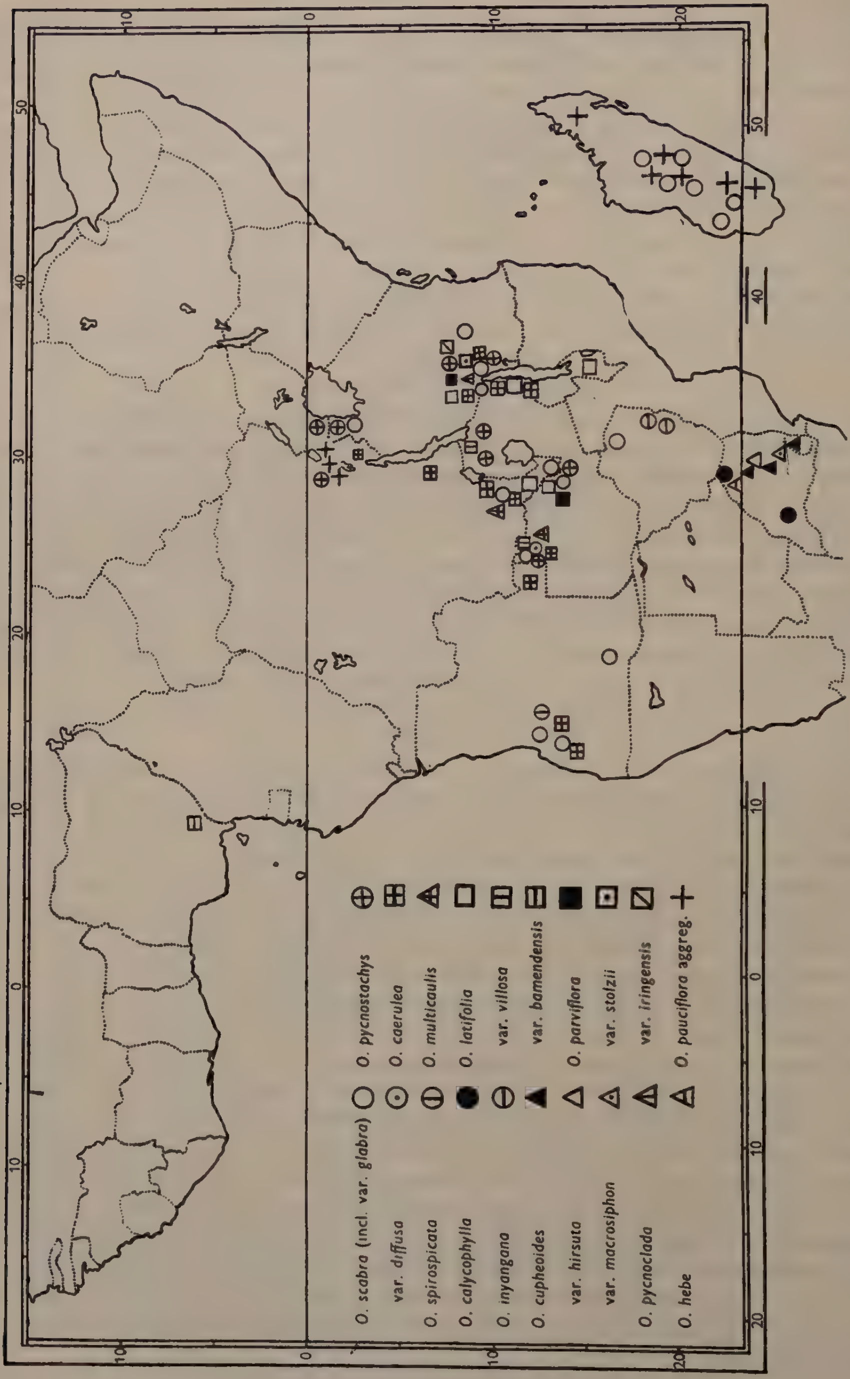

Fig. 1. Distribution of the species of *Otiophora*.

throughout the range of the genus. Evolution seemed to take place in three main lines, each from a particular variation of *O. scabra*. During this evolution the inflorescence has progressed towards the head type. *O. scabra* var. *diffusa* is closely related to the typical form in flowers and inflorescence but differs in its straggling habit. *O. pauciflora* would appear to have evolved somewhat on these lines. It is possible that var. *burttii* evolved independently on the mainland, and merely resembles *O. pauciflora* by convergence. Another group consists of woody species, often suffruticose in habit, and of these *O. calycophylla* resembles *O. scabra* in its small flowers but shows some affinities with the bigger-flowered *O. cupheoides–O. inyangana* group on the one hand, and clear affinities with *O. hebe* on the other. This species has larger flowers and *O. pycnoclada*, which is closely related to *O. hebe*, has still larger flowers. It is characteristic of this group that evolution in the flower is to larger forms. The varieties of *O. cupheoides* also demonstrate this. Of the third line of evolution divergence occurred early in *O. spirospicata*, *O. pycnostachys* and *O. caerulea* and these three are very well marked. They have large flowers, but only *O. caerulea* has completely lost all trace of the spicate inflorescence. It is related in habit to the 'caespitose' group, *O. multicaulis*, *O. parviflora* and *O. latifolia*, which have retained the primitive character of small flowers but have quite lost the spicate inflorescence. In the writer's opinion they represent the least well-defined species in the genus and form what might be called the 'growing point' of the genus. This arrangement, which is of course largely hypothetical, is shown in Fig. 2.

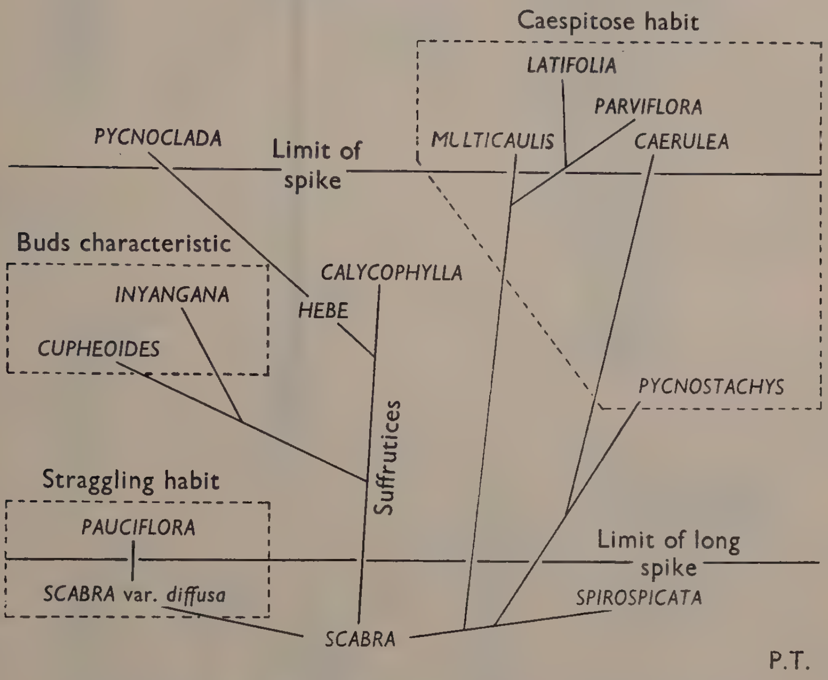

Fig. 2. Suggested phylogenetic scheme for the species of *Otiophora*.

KEY TO THE SPECIES OF *OTIOPHORA*

Notes on the use of this key. It must be remembered that in immature plants the inflorescence characters are under-developed and it may be impossible to decide whether or not it will eventually be a spike. It is important that flowers should be carefully dissected so that an accurate knowledge of them is available. Unless this is done such different characters as 'hairy throat' and 'filaments with hairs at base' will easily be

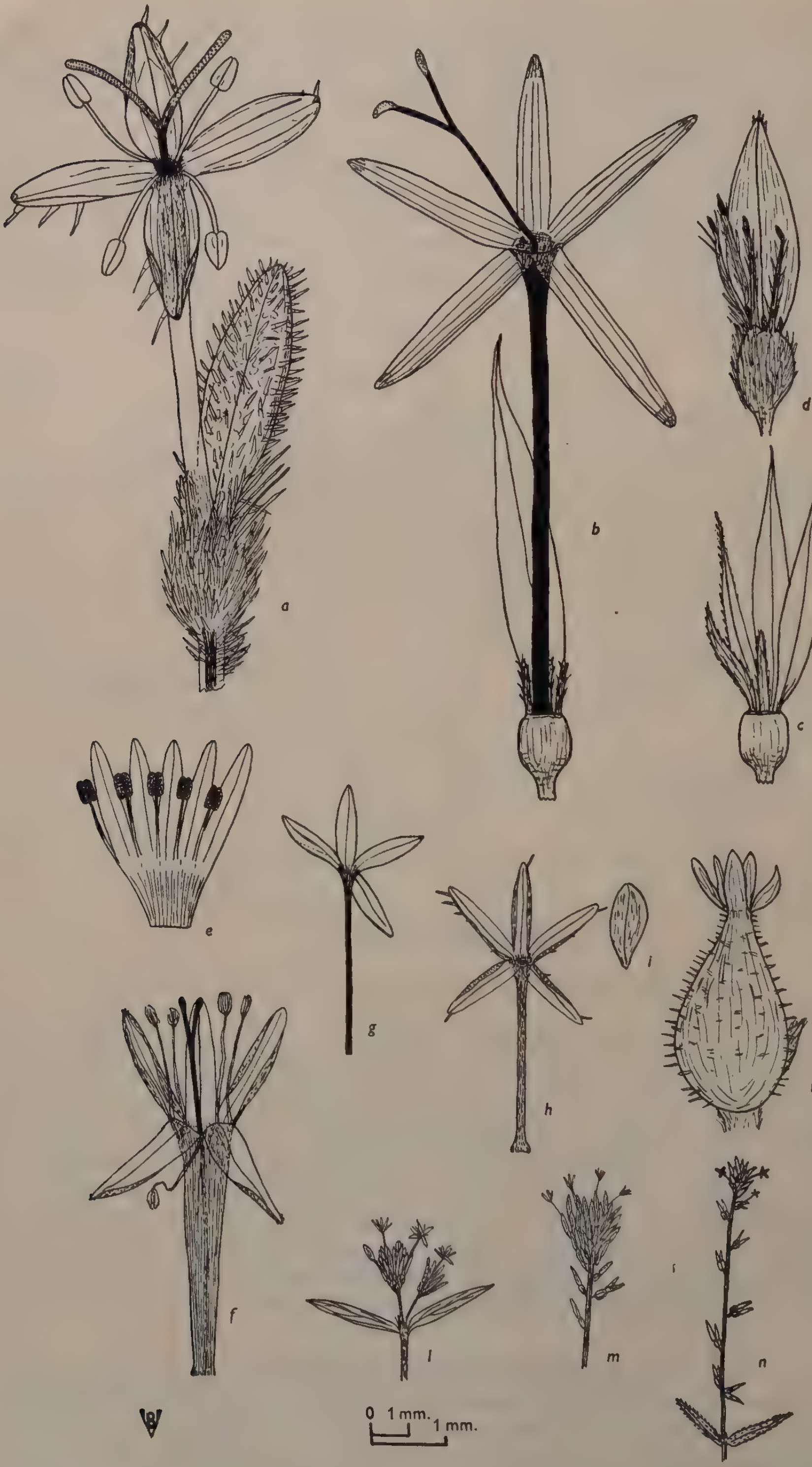

Fig. 3. For legend see p. 389.

confused. Similarly, it is often difficult to make out the shape of the buds in dry material. Corolla descriptions and measurements refer to living or boiled material, and not to dry material. Measurements of style length include stigmas as well. With reference to the bud characters the statement 'buds with limb abruptly expanded into a head and clearly distinct from the filiform tube' refers to buds of the shape shown in Fig. 4*c*–*i*, and the statement 'buds with limb merging into tube' refers to buds of the shape shown in Fig. 4*a*, *b*, *k* and *n*. These species clearly have a much less filiform corolla tube. These bud characters are quite easy to see and there is little variation. Although the latter type of bud may sometimes be of the shape shown in Fig. 4*b*, *k* it is never like Fig. 4*c*–*i*. Deformed flowers due to galling by mites (?) are not infrequent, particularly in material of *O. scabra* from Rhodesia. This galling completely alters the shape of the buds and corollas, but there are usually a few ungalled flowers present, and by the aid of these the identity of the plant may readily be ascertained. Several species occur in the key twice, since the inflorescence is variable. Roman numerals following the names refer to the check list and order of the species, and are used to avoid confusion with the key digits.

1 Mature inflorescence a lax spike, 6–15 cm. long (Fig. 3*n*), but if shorter and more condensed (Fig. 3*m*) then buds with limb distinct from tube (Fig. 4*c*–*i*). 2
Mature inflorescence usually a head, sometimes only consisting of a few flowers at apex of shoot, but if a short spike (up to 5 cm.), then buds with limb merged with tube (Fig. 4*a*, *b*, *k* and *n*). 8

2 Filaments with hairy appendages at base or hairy at base. 3
Filaments without hairs of any kind. 4

3 Spike very short if present, and not at all lax. *O. pycnostachys* (viii) (see also couplet 11)
Spike long and lax. *O. spirospicata* (ii)

4 Plant a straggler. Flowers usually in small heads, or short dense spikes up to 3 cm. long. Corolla tube 6–12 mm. long, lobes 4–5 mm. long. *O. pauciflora* aggr. (xiii) (see also couplet 15)
Plant erect or if straggling then flowers smaller. Corolla tube 3–6 mm. long, lobes 2–2·5 mm. long. 5

5 Leaves small, 8 × 2 mm., crowded at the apices of shoots. Internodes barely exceeding 1–2 mm. Spike if present 1–2 cm. long. *O. hebe* (vii) (see also couplet 14)
Leaves larger, or if small then some internodes even near apices of shoots at least 1–1·5 cm. long. 6

6 Flowers usually white in small heads or in short spikes about 2 cm. long. Leaves up to 1·4 × 0·5 cm. *O. calycophylla* (iii)
Flowers usually reddish in long lax spikes up to or exceeding 15 cm. Leaves larger, nearly always some present which exceed 2 cm. in length. 7

7 Plant erect. Calyx tube with long white outstanding hairs (var. *glabra* differs only in glabrous leaves). *O. scabra* (i)
Plant straggling, leaves larger, 2·5–4·5 cm. long, 0·6–2 cm. broad. Calyx tube pubescent only. var. *diffusa* (i*b*)

8 Buds with the tube distinct from the limb. Flowers in quite definite heads. 11
Buds with the tube merged with limb. Flowers in heads or heads plus spikes. 9

9 Throat of corolla hairy. *O. inyangana* (aggr., iv)
Throat of corolla glabrous. 10

Fig. 3. *a*, flower of *Otiophora parviflora* (from Type). *b*, flower of *O. caerulea* (stamens omitted—from Milne-Redhead 4388). *c*, calyx of ditto to show variation in lobes (from Stolz 1947). *d*, calyx of *O. pycnoclada* (from Goetze 965). *e*, 5 mm. long bud of *O. cupheoides* opened (from Berg Plateau, Mudd s.n.). *f*, corolla with withered stamens (from same plant). *g*, corolla of *O. calycophylla* (stamens omitted—Nation 216 and 94). *h*, corolla of *O. scabra* (stamens and style omitted—from Type No.). *i*, 'petal' of abnormally polypetalous flower of *O. scabra* (from Scott Elliot 1790). *k*, advanced stage of corolla tube gall of *O. scabra* (Eyles 8047). *l*, diagram of head-like inflorescence. *m*, diagram of head-like inflorescence with a few flowers arranged in a spike beneath. *n*, diagram of a spike inflorescence. (N.B. The upper scale refers to Fig. 3*b*–*k*, the lower scale to Fig. 3*a*, and Fig. 3*l*–*n* are not to scale.)

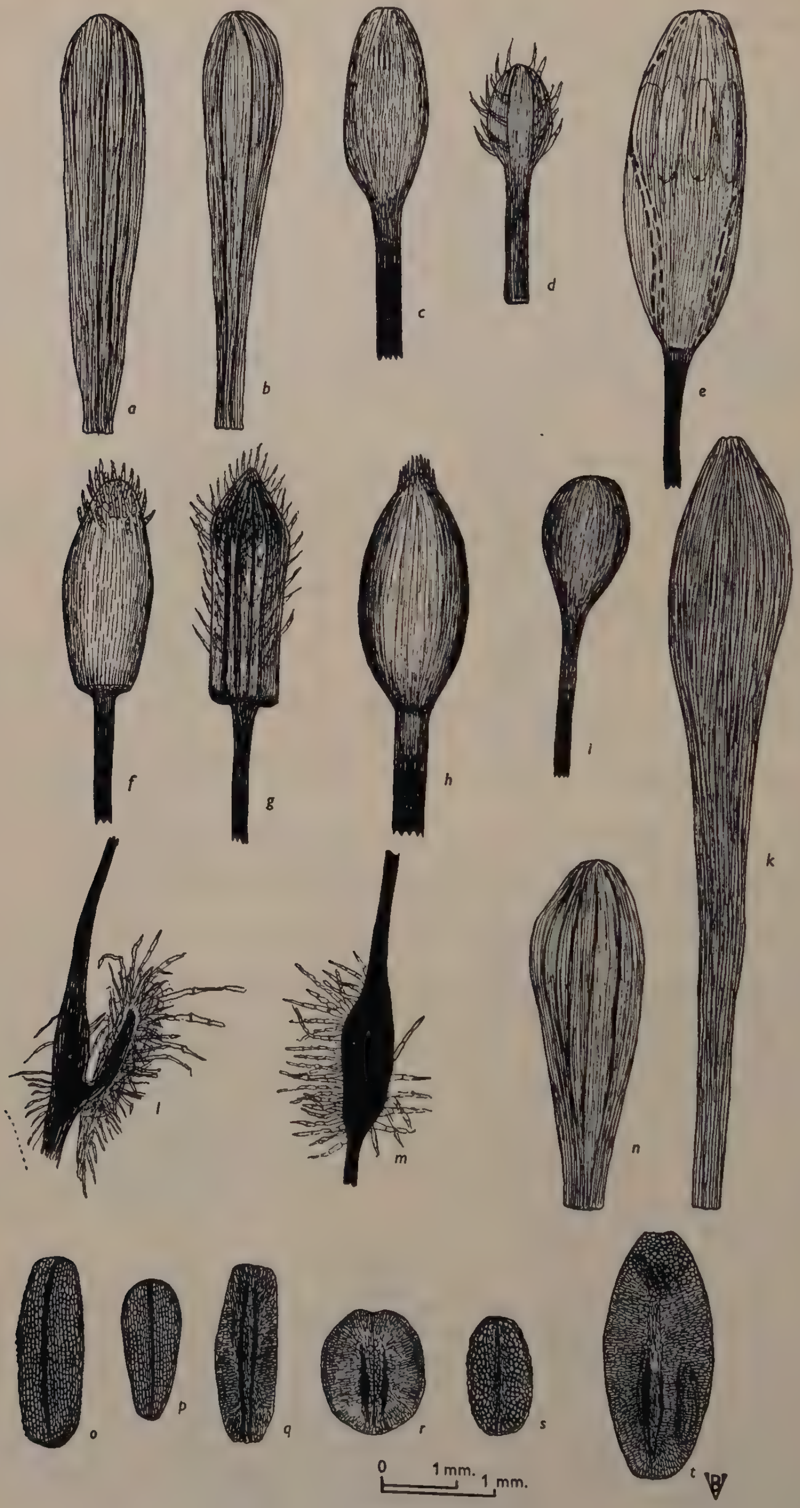

Fig. 4. For legend see p. 391.

10 Corolla tube 5–6 mm. long, leaves glabrescent. *O. cupheoides* (v)
Corolla tube 10–11 mm. long, leaves glabrescent. var. *macrosiphon* (v*b*)
Corolla tube 6–8 mm. long, leaves densely hairy. var. *hirsuta* (v*c*)

11 Leaves linear to linear-lanceolate, whorled. Filaments hairy at the base. *O. pycnostachys* (viii)
Filaments glabrous at the base. **12**

12 Corolla tube very filiform, up to 12 mm. long, lobes usually narrow, 5 mm. long. Calyx tube rather globose, glabrous. Seeds almost globose. Leaves variable, 3–4 cm. long. *O. caerulea* (ix)
Plant without the above characters combined. **13**

13 Leaves glabrous, subcoriaceous, equal, sessile and very closely placed at the apices of shoots. Stem leafless below with small sheaths at nodes. Internodes ± 1–2 mm. **14**
Leaves not so closely placed, nor subcoriaceous, often hairy. **15**

14 Leaves 9–10 × 3–4 mm. Corolla lobes 5 mm. long. *O. pycnoclada* (vi)
Leaves 8 × 2 mm. Corolla lobes 2·5 mm. long. *O. hebe* (vii)

15 Erect or small semiprocumbent herbs. Seeds ovoid or globose. Corolla small, tube 3–6 mm. long, lobes 1·5–3·5 mm. long. **16**
Straggling plants, variable in size, with usually 2–3 long shoots. Seeds oblong-elongate or tapering-elongate. Corolla tube 6–12 mm. long, lobes 4–5 mm. long, rarely only 3 mm. *O. pauciflora* aggr. (xiii)

16 Plant suberect or procumbent, small, 7–15 cm. high. Leaves ± ovate acute, broadest at base or middle, abruptly contracted or gradually narrowed to base, 10–19 × 6–11 mm. **17**
Plant erect, 8–20 cm. high. Leaves ovate-lanceolate to linear, 13–27 × 3–8 mm., *or* if ovate then leaves small, 9–12 × 3·5–4·5 mm. **18**

17 Tube 5–6 mm., lobes 2–3 mm. glabrous. Leaves and foliaceous lobes of calyx glabrescent or with multicellular hairs (stem and leaves very hairy in var. *villosa* (xi*b*)) *O. latifolia* (xi)
Tube 4 mm. long, lobes 1·5 mm. long, with a few long hairs on lobes and buds. var. *bamendensis* (xi*c*)

18 Plant with numerous (20–50) shoots from a very woody rootstock 5–8 mm. in diameter. Leaves small, ovate to ovate-lanceolate, 9–12 × 3·5–4·5 mm., glabrous or glabrescent. Calyx tube glabrous or with short hairs. *O. multicaulis* (x)
Plant with fewer (up to 20) shoots from a less woody rootstock 2–4 mm. in diameter. Leaves ovate-lanceolate to linear, 13–27 × 3–8 mm., glabrescent to hairy. Calyx tube with long white hairs. **19**

19 Leaves ovate-lanceolate. Buds and corolla lobes with long hairs. *O. parviflora* (xii)
As above, but buds and corolla lobes glabrous, mauve. var. *iringensis* (xii*c*)
Corolla lobes and buds glabrous. Leaves linear-lanceolate to linear. var. *stolzii* (xii*b*)

ENUMERATION OF THE SPECIES

1. **Otiophora scabra** Zuccarini, in *Abh. Akad. Muench.* **1**, 315 (1832). *Pentanisia spicata* S. Moore in *J. Bot., Lond.*, **46**, 38 (1908). (This mistake was corrected in *J. Bot., Lond.*, **46**, 76.) (General study, Fig. 5; corolla, Fig. 3*h*; seed, Fig. 4*s*.) *O. scabra* is figured in Drake del Castillo, *Histoire Nat. de Plantes*, Tome IV, Pl. 412; in Grandidier, *Hist. de Madagascar*. The calyx alone is figured in Engl. and Prantl, *Die nat. Pflanzenf.*, IV, **4**, fig. 42 F.

This species, by far the most widely distributed of the genus, was minutely described by Zuccarini in an excellent description very much more accurate and detailed than any

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Fig. 4. *a*, bud of *Otiophora inyangana* (from Type). *b*, ditto to show effect of drying. *c*, portion of bud of *O. latifolia* (from Type). *d*, bud of *O. parviflora* (from Type). *e*, portion of bud of *O. caerulea*—broken lines show variation in outline of limb (from Marks 77). *f*, portion of bud of *O. pauciflora* (from Type). *g*, portion of bud of *O. pycnostachys* (from Type No.). *h*, portion of bud of *O. spirospicata* (from Type No.). *i*, portion of bud of *O. calycophylla* (from Burke 94). *k*, bud of *O. cupheoides* var. *macrosiphon* (from Type). *l*, base of filament of *O. spirospicata* (from Type No.). *m*, ditto *O. pycnostachys* (from Lejeune 239). *n*, bud of *O. cupheoides* (from Berg Plateau, Mudd s.n.). *o*, dorsal surface of seed of *O. pauciflora* (Scott Elliot 2027). *p*, ditto, var. *burttii* (Robyns 2385). *q*, ditto *O. pycnostachys* (Hutchinson & Gillett 3835). *r*, ditto *O. caerulea* (Whyte 193). *s*, ditto *O. scabra* (Type No.). *t*, ditto *O. spirospicata* (Type No.). (N.B. The upper scale refers to all figures with the exception of 4*l*, *m*. The lower scale refers to these.)

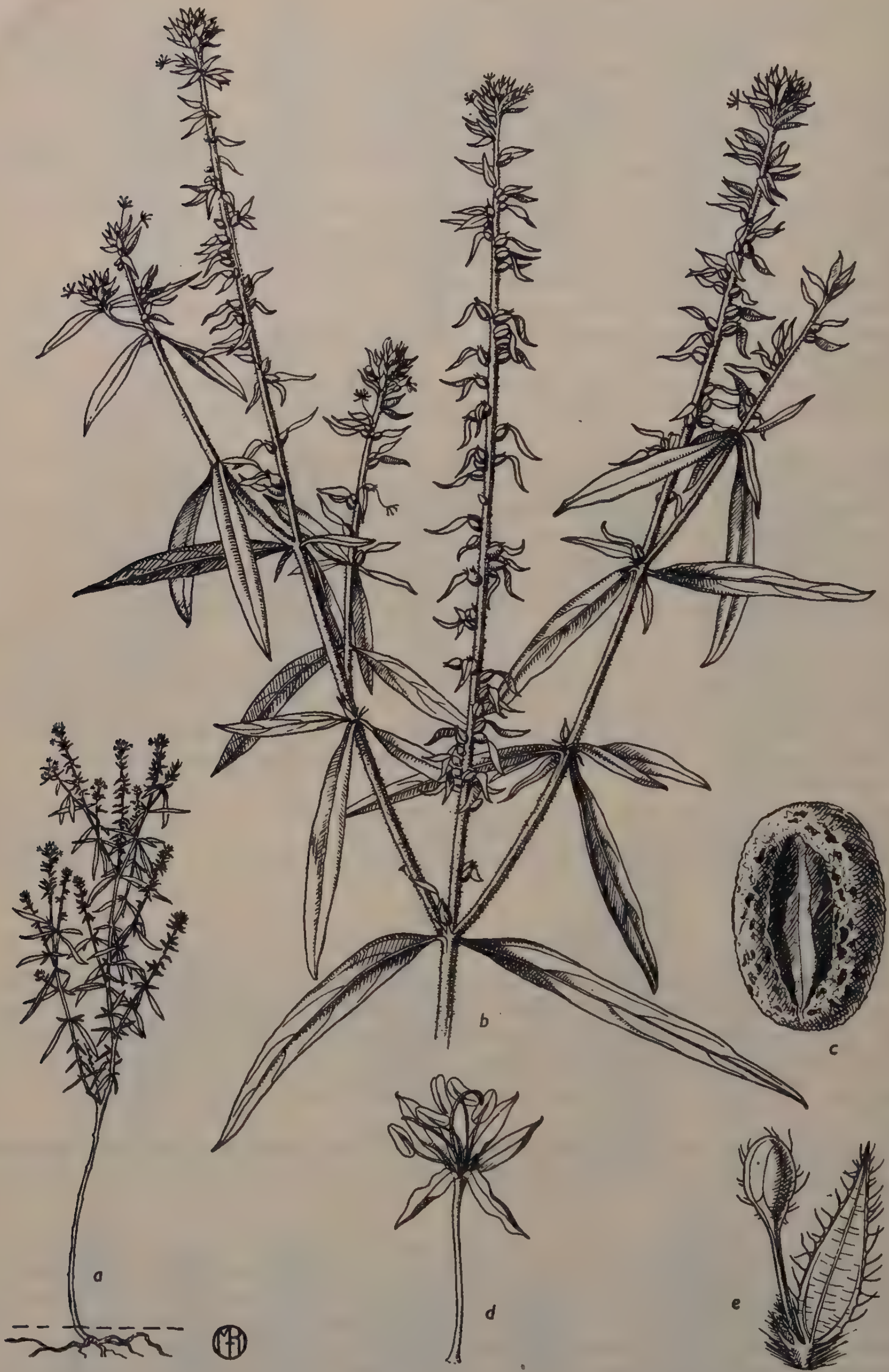

Fig. 5. *Otiophora scabra* Zucc. *a*, whole plant, × $\frac{1}{6}$. *b*, upper portion, natural size. *c*, seed, × 20. *d*, corolla, × 7. *e*, bud and calyx, × 7. (From Schlieben 1951.)

subsequent descriptions published of other species in the genus. Although very variable in habit and leaves, it is a very characteristic plant.

Annual (rarely perennial?) herb or undershrub. *Stem* slender, erect, and much branched, woody at the base, or stem branches numerous, arising close together from the main stem near to the ground thus giving the plant a caespitose appearance. The tufted forms may not exceed 15 cm. in height, but the more usual slender forms vary from 15 to 75 cm. and may exceed this. Stem terete or somewhat angular, usually dark, epidermis frequently peeling and revealing paler colour beneath. Woody basal part of stem 2–4 mm. in diameter, unbranched and leafless for 4–10 cm. *Rootstock* consisting of one tapering main root, continuous with the woody base of stem. Lateral roots few, much slenderer than main root. Branches covered with dense white scaly hairs above, but glabrescent below, where the epidermis has hardened and begins to flake away. The density of this indumentum varies considerably. *Internodes* variable, 1–4 cm. long, shortest in the caespitose forms. *Stipules* small, fimbriated; segments 3–4, brown, setiform, ±2 mm. long. *Leaves* sessile or minutely petiolate, paired, opposite, sometimes appearing verticillate owing to the presence of very abbreviated axillary shoots, lanceolate to linear-lanceolate, 1–5 cm. long × 2–6 mm. broad, discolorous, dark green above, pale green below, densely covered with adpressed, scaly, white multicellular hairs above but becoming glabrescent with age. Leaves acute, somewhat revolute at edges. Lateral nerves 4–5 on each side of the midvein, often pale brownish, clearly visible below, invisible or scarcely visible above. *Flowers* red or mauve, geminate in spikes terminating the branches, the internodes between the flower pairs varying from 1 to 10 mm. Adult spikes up to or exceeding 15 cm., ebracteate. Pedicels very minute, only visible as persistent woody protuberances after the fruits have dropped off, flowers and fruits appearing quite sessile. *Calyx tube* ovate ±1 mm. long, densely covered with white bristly outstanding hairs. Calyx lobes 5; one lobe foliaceous, discolorous, with one main nerve visible (two others are actually present), lanceolate, broadest near base and gradually tapering to an acute apex, 3–5 mm. long × 1–2 mm. broad, margin entire, revolute, with white bristly scaly hairs on both sides; rest of lobes small or minute, unequal, densely hispid. *Buds* with limb abruptly expanded into an ovoid head, with scattered multicellular hairs. *Corolla tube* extremely filiform, 3·5–6 mm. long ±0·2 mm. wide, slightly wider at the ends, glabrous. Throat glabrous. Corolla lobes 4–5, lanceolate, somewhat obtuse, about 2–2·5 mm. long and 0·5–0·75 mm. broad, with long multicellular hairs towards apex of outer surface, and with three main veins and several lateral ones. The indumentum of the corolla lobes is variable. *Stamens* 4–5, exserted for about 2 mm., filaments filiform, glabrous, anthers ovate, fixed somewhat below their middle, 0·75 mm. long × 0·5 mm. broad. Pollen grains subglobose, $\pm 35\mu$ diameter. Style filiform, stigma bifurcate, lobes filiform but slightly flattened, 1–1·5 mm. long, style and stigma together exserted for a distance equal to the length of the corolla lobes. *Fruit* pale yellow brown, densely covered with white hairs, 2 mm. long × 1·5 mm. broad. Seeds black, ovoid, about 1·4 mm. long × 0·9 mm. broad (sometimes smaller, particularly on the mainland), ventrally flattened, granulated, slightly keeled dorsally, and with a linear depression surrounding the hilum.

The flowers of East and Central African individuals of this species are particularly prone to be galled by a mite. The corolla tubes thicken and become very hairy. Eventually they become greatly enlarged and conical, crowned at the apex by the aborted corolla lobes (Fig. 3*k*). Another pathological form of flower was found in *Scott Elliot* 1790. In many of the flowers the corolla tube was quite absent, and the corolla was reduced to over a dozen small irregular lobes thus making the flower appear polypetalous (Fig. 3*i*). A third and very peculiar pathological form is represented by three sheets from Madagascar. In inflorescence this form, which may be designated aberration *stricta* for reference purposes, is very distinct from typical material, and since it is not at all obviously pathological, one would imagine it to be at least a distinct variety. The inflorescence is much more condensed and strict. Whereas in typical *O. scabra* the inflorescence is a normal raceme, i.e. young buds at apex, open flowers in middle and fruits at the base in the aberration nearly all the flowers are buds, apart from a few normal flowers which give rise to fruits. This is most distinctive and if these buds are opened it is found that the gynaecium has become a pair of flattened mucronate laminae, and in some cases all of the stamens are leaf-like as well. These buds do not develop. Whether this is a mutation affecting the majority of flowers or whether it is a disease produced by some external causal agent can only be decided in the field. The few normal fruits contain seeds which are absolutely typical of *Otiophora scabra*. The specimens in question are:

MADAGASCAR. Tananarive District: Ambohimianga, dry places, 27 March 1921, *Decary* 649 (P.). Near Tananarive, April 1922, *Waterlot* 488 (P.). Near Ambatofimandrahana, humid places on schist, flowers rosy white, 1600–1800 m., 20 February 1938, *Decary* 13117 (P.). Such abnormalities may render the naming of certain plants difficult but normal flowers can usually be found if searched for. *O. scabra* is the most widely distributed species of the genus but would appear to be rather rare on the African mainland. It occurs in the mountainous districts of central Madagascar, and on the mainland reaches its limits in northern Tanganyika, western Angola, and the north-eastern portion of Southern Rhodesia.

BELGIAN CONGO. Katanga: Kitimbo village, just inside Congo border, 15 January 1908, *Kässner* 2290 (K.) and *Kässner* 2289 (B.M.). Kisanga canal, Upper Katanga region, June 1935, *Quarré* 4539 (K.) and *Quarré* 1539 (B.).

TANGANYIKA. Bukoba District: near Nyakato, rocky place at 4000 ft., flowers red, August 1931, *Haarer* 2133 (K.). Bukoba, *Stuhlmann* s.n. (K.). Sali, about 35 km. south of Mahenge, in savanna and bushland at 900–1000 m., 22 March 1932, *Schlieben* 1951 (K., P. and B.M.). Rungwe District: Mulinda, flowers rose, 22 July 1912, *Stolz* 1457 (K.). Mwasukulu, 900 m., 'fruit' green-red (actually his so-called fruits are galled corollas), 1 July 1911, *Stolz* 783 (K.).

NORTHERN RHODESIA. Mufulira, small bush on clay bank above pond, flowers galled, 11 June 1934, *Eyles* 8047 (K. and S.). Mwinilunga District, near source of R. Matonchi, on bare ground in clearing in *Cryptosepalum* woodland on sand, erect bushy annual, leaves deep green, corolla mauve, 7 October 1937, *Milne-Redhead* 2629 (K., duplicates at Brussels and Pretoria). Niamkolo, S. of Lake Tanganyika, *Carson* (K.).

NYASALAND. North Nyasa, 1896, *Whyte* (K.).

SOUTHERN RHODESIA. Enterprise District, flowering March, flowers galled, *Eyles* 6918 (K.). Mazoë, Iron Mask Hill, 5000 ft., flowers pink, January 1915, *Eyles* 604 (K., S. and B.M.). Mazoë, Iron Mask Hill, 5200 ft., *Eyles* 522 (B.M. and S., TYPE of *Pentanisia spicata* S. Moore).

ANGOLA. Huila (data obtained from Hiern, *Cat. Welw. African Plants*, 1, 499): in sandy thickets about Lopolo and Humpata, flowers December 1859, fruit January 1860, *Welwitsch* 5330 (K., P. and B.M.). Ferrão da Sola, April 1860, *Welwitsch* 5331 (K. and B.M.). Humpata, flowers and fruit at end of January 1860, *Welwitsch* 5336 (K. and B.M.). Bié: chiefly in 'Mucuve' [*Cryptosepalum pseudotaxus*] woods, Masacallas of Cassuango, Cuiriri, *Gossweiler* 3413 (K. and B.M.).

MADAGASCAR. The divisions employed here for the subdivision of this territory are those used for the 1 : 500,000 maps published by the War Office in 1942 (4th edition). Flowers reddish or bluish unless otherwise stated.

Locality vague, undecipherable or not located on map. CENTRAL MADAGASCAR: *Baron* 3693, 2436, 3342, 962 and 2429 (K. and P.) and 734 (K.). Ditto, February 1882, *Parker* (K.). Ambaradondrazaka, 6 December 1877, *Rutenberg* (P.). Am Berge, Abeloma, 13 January 1878, *Rutenberg* (P.). Ampesokely? damp wood, 11 March 1917, *Decary* (P.). 'Madagascar', *pre*-1867, *Lyall* (K.). Andrainitoro, rocks and rocky hillocks, January 1892, *Geneaud* 47 (P.). TANANARIVE: Emirna, arid ground on open sunny mountains, *Bojer* (Type in Herb. DC., duplicates K., P. and V.). The Kew sheet does not bear Bojer's name, but the label is in his handwriting. Imerina, in grass, sunny slopes, January 1881, *Hildebrandt* 3846 (K. and P.). Imerina, Tamatave to Tananarive, grassy places, January 1889, *Scott Elliot* 1790 (K. and P.). Tan(n)anarive: ex Hb. *Justice Blackburn* (K.). Ankafana, 1880, *Deans Cowan* (P.). Analamozoatra, 800 m., *Perrier de a Bâthie* 6938 (P.). Tananarive, 1912, *Perrier* 4024 (P.). Basin of R. Mangoro, open places by borders of roads, on gneiss, 800 m., flowers white or violet, August 1912, *Perrier* 3900 (P.). Tampoketsa, to north of Ankazobe, forests of Ambohilantely and nearby, 1600 m., October 1933, *Humbert* 11058 (P.). Near Moramanga, 900 m., 26 October 1912, *Viguier & Humbert* 1032 (P.). District of Manyakandriana: Angavo, March 1923, *Waterlot* 705 (P.). Between Ambohimanga and Batsitra, open country, October 1906, *D'Alleizette* 355 (P.). Tananarive, hillocks and rocks, December 1892, *Geneaud* (P.). Ambohimanga, April 1921, —? 99 (P.). Between Tananarive and Miarinarivo, rocks, 20 March 1930, *Decary* 7662 (P.). South of Moramanga, woody marsh, 10 February 1930, *Dec.* 6945 (P.). Moramanga, sunny place, 21 February 1930, *Dec.* 7229 (P.). Tananarive, Amkatso, dry bush, 21 January 1921, *Dec.* 709 (P.). Andraisoro, dry places, 20 February 1917, *Dec.* .n. (P.). Tampokatsa to the north of Ankazobe, sides of road, 13 March 1930, *Dec.* 7507 (P.). Angavo close to Ankazobe, rocks, 8 March 1930, *Dec.* 7288 (P.). Massif de 'Angavo, near Ankazobe, sunny slopes, 10 March 1930, *Dec.* 7313 (P.). Morondava: Mahabo, dry places on basalt soil, 30 January 1889, *Scott Elliot* 1925 (K.). Ambositra: near Antsirabe, hill of Tapia (Haute Sahatsio), siliceous rocks, *c.* 1600 m., 24 December 1928, *Humbert* 7127 (P.). Same locality, 20 July 1928, *Humbert & Swingle* 4666 (P.). Prov. Vakinankaratra, district of Antsirabe, mountain to the west of Ambohiponanana, 1600 m., flowers yellowish white (pathological), 20 November 1912, *Viguier & Humbert* 1439 (P.). Near Antsirabe, wood of Tapia, laterite, 1600 m., October 1913, *Perrier* 3846 (P.). Mangoky: Plateau of Isalo to the west of Ranohira, siliceous rocks (sandstone), 300–1000 m., 30 July 1928, *Humbert & Swingle* 5037 (P.). Isalo, 500 m., July 1910, *Perrier* 3883 (P.). Isalo, Ambatolaky, 1000 m., July, *Perrier* 4432 (P.). Fianarantsoa: Andringitra, amongst *Philippia*, 1400 m., March 1922, *Perrier* 14444 (P.).

Many of the plants cited above have glabrescent leaves, possibly in old specimens due o rubbing. The following variety has, however, the leaves quite glabrous. It is a western orm in distribution.

O. scabra Zucc. var. **glabra** var.nov., ab *O. scabra* typica, foliis glabris, corollis et alycis lobis glabrescentibus differt.

Erect annual herb. Stem somewhat angular. Leaves glabrous 5 × 0·5 cm. Calyx tube hairy. Foliaceous calyx lobe and corolla lobes glabrescent. Corolla tube deep mauve, obes recurved, mauve. Filaments mauve and anthers orange-yellow.

ANGOLA. Moxico District, among rocks in sandy ground between R. Lupula and R. Kanyezhi, one young plant with primary leaves 8 × 1 cm., 20 January 1938, *Milne-Redhead* 4254 (K. Type, duplicate at Brussels). Huilla, in the drier thickets near Lopolo and around the L. Ivantâla in wooded situations in the direction of Quilengues, bundant, flowers and young fruit, March 1880, *Welwitsch* 5329 (K. and B.M.). (N.B. *Welwitsch* talks of the throat as very densely bearded with white hairs, whereas he writer finds none in the flowers of this number which he has dissected. The escriptions of 5329 in Hiern, *Cat.*, p. 499, do not agree with the plants at K. or the B.M.) Minnesera, by R. Longa, 1250 m., flowers carmine, very rare, March 1900, *Baum* 689 (K.). Benguela, in special shady localities on the mountains of Ferreira do Amaral, *Gossweiler* 2884 (K. and B.M.).

O. scabra Zucc. var. **diffusa** var.nov., ab *O. scabra* typica habitu procumbente differt. *Herba* vagans. *Internodia* 2–6 cm. longa. *Rami* teretes, pilosi, pallide brunnei. *Folia* ilis parvis parcis obtecta, 2·5–4·5 cm. longa, 0·6–2 cm. lata. *Calycis* tubus pubescentia ndutus. *Spicae* usque 16 cm. longae. Corolla et filamenta lilacina, antherae et styli lbi. Cetera ut in *O. scabra*.

NORTHERN RHODESIA. Mwinilunga District, straggling amongst shrubs in evergreen vegetation around slowly seeping water at source of R. Matonchi, 19 Decembe 1937, *Milne-Redhead* 3740 (K. Type, duplicates at Brussels and Pretoria).

This very distinct variety shows affinities with *O. pauciflora* in its habit, but differs i inflorescence and small flowers. It differs from typical *O. scabra* in its larger paler an more glabrous foliage, less hairy calyx tube, and paler and rounder stem, as well as by it totally different habit. Further material will probably show that this form is best considered as a new species, but for the present it is given infra-specific rank, as variety.

2. **Otiophora spirospicata** Good in *J. Bot., Lond.*, **64**, Suppl. 2, 40 (1926). (Bud Fig. 4*h*; seed, Fig. 4*t*; and filament, Fig. 4*l*.) Erect perennial herb, about 80 cm. high woody at the base. Good describes it as a perennial herb or undershrub with a much branched rootstock. *Stems* terete, glabrous, brown, striate, with basal 30 cm. almos leafless. *Stipules* ± quadrifid, fimbriae subulate *c.* 3 mm. long. *Leaves* lanceolate, subsessile 3·5–7 cm. long, 0·9–2 cm. broad, shining olive green above, paler yellow green below entirely glabrous, with 4–5 lateral veins on either side of the midvein. *Flowers* white geminate, pairs spirally arranged on spikes up to 7–10 cm. long. These spikes are sometimes sparingly pubescent in places. The distance between pairs of flowers varies from 1 to 10 mm. Fruiting pedicels woody, persistent, ±2 mm. long. *Calyx tube* elongate glabrous, with one foliaceous lobe 6×2 mm. and four minute almost obsolete teeth, o with one foliaceous lobe 6×2 mm., one smaller foliaceous lobe 3×0·5 mm. and three minute teeth, all glabrous or with very few marginal scaly hairs. *Buds* with limb abruptly expanded into an ovate head, distinct from the filiform tube, with a very few scaly hairs a extreme apex. *Corolla tube* 6–7 mm. long, 0·35 mm. broad; lobes 5, 4 mm. long, 1 mm broad, with a few scaly hairs at apices, and with three veins. *Stamens* exserted for abou 4 mm., filaments with very hairy projections *c.* 1 mm. long, at the base, close to the poin of insertion in the throat. Anthers ovate, *c.* 1 mm. long. Style 13–14 mm. long, stigma shortly bilobed, lobes ±0·5 mm. somewhat thickened. *Mature fruit* oblong, 5 mm long×1·6 mm. broad, slightly curved, brown, glabrous, and striate. Seeds black, granulated, ovate, depressed so as to be markedly concavo-convex in section, 3·2 mm. long 1·4 mm. broad (i.e. larger than those of any other known species of the genus). This very distinct species, clearly distinguished from the others by its inflorescence, filament projections, fruits and seeds, is known only from the type gathering.

ANGOLA. Bié District, on the rocky river banks of R. Cuiriri, flowering in February *Gossweiler* 4103.

3. **Otiophora calycophylla** (Sonder) Schltr. et K. Schum. in Engl. *Jahrb.* **30**, 416 (1901) *Anthospermum calycophyllum* Sonder, *Flora Capensis*, **3**, 31 (1865). *Otiophora calycophylla* (Sonder) Hutch., *A Botanist in Southern Africa*, p. 671 (1941). (Bud, Fig. 4*a* corolla, Fig. 3*g*.) This species was transferred to *Otiophora* by K. Schuman, and he wa undoubtedly correct in doing so, but he wrongly identified it with *O. cupheoides* N. E Brown, and the author of the latter species evidently agreed with him since some of th sheets of *O. cupheoides* have the name *Anthospermum calycophyllum* added as a synonym in his handwriting. The two species though related are clearly distinct. The flowers o *Otiophora calycophylla* are smaller than those of *O. cupheoides*, and the corolla tube i uniformly filiform and not dilated at the top (Fig. 3*f*, *g*). The buds are quite different those of *O. calycophylla* having the limb expanded into a pyriform or oval head. Thi expansion is not quite so abrupt as in the majority of the species, but is quite differen from the shape encountered in *O. cupheoides* and *O. inyangana*.

Erect perennial herb or undershrub, 20–30 cm. high. *Stem* woody, much branche near the base, dark brown, irregularly striate, glabrescent. Branches slender, covere with scaly hairs but becoming glabrescent, noduled at nodes by persistent stipules an petioles. *Stipules* small, fimbriate. *Internodes* variable, but some of 0·7–1·5 cm. alway present even at the apices of the shoots. *Leaves* small, often slightly coriaceous, shortl petiolate (petioles 0·5–1 mm. long), ovate to ovate-lanceolate, broadest near base or at middle, and contracted suddenly or gradually to base, mostly 0·5–1·5 cm. long, 2–4 mm. broad, acute or somewhat obtuse, hairy or glabrescent. The glabrescent forms have very short bristly hairs on the upper surface of the leaves, towards their apices. Sonder describes the leaves as glabrous, though the type is hairy. *Flowers* white or mauve, geminate in short spikes *c.* 2 cm. long, condensed at the apices into heads. *Calyx tube* ovate, *c.* 1 mm. long, shortly pubescent. Calyx lobes 5, one foliaceous, ovate-lanceolate, acute, 3 mm. long, 1–1·5 mm. broad, margin somewhat ciliate, lamina glabrous or with few scales, other four minute, almost obsolete. *Buds* with limb expanded into a pyriform head distinct from tube. Corolla tube uniformly very filiform, 4–5 mm. long, 0·2 mm. wide, lobes 5, 2–2·5 mm. long, glabrous. *Capsules* ovoid, pale brown, shortly pubescent, 2 mm. long, 1·3 mm. broad. Seeds blackish, small, elongate, 1·1 mm. long, 0·4 mm. broad (may not have been quite mature). This species has so far only been seen by the writer from the Transvaal, but Sonder cites two Natal specimens without any data.

TRANSVAAL. Rustenberg District: Magalisberg, *pre*-1854, *Zeyher* 1376 (K., cited by Sonder). Magalisberg, November *pre*-1864, *Burke* 94 (K., cited by Sonder). Magalisberg, growing in kloop, blossom white, leaves dark green, 4500 ft., 1905, *Nation* 216 and 64 (K.). Zoutpansberg above Louis Trichardt, flowers mauve, 16 December 1928, *Hutchinson* 2018 (K.). Transvaal, without further data, *Sanderson* s.n. (K.).

4. **Otiophora inyangana** N. E. Brown, in *Kew Bull.* **1906**, 107. (Buds, Fig. 4*a*, *b*.) This variable species is related to *O. cupheoides* and the paired-leaved forms often closely resemble the latter. The leaves are, however, usually in whorls of three and the throat of the corolla is always hirsute. The bud shape is very similar in both species.

Erect perennial herb or undershrub, 20–60 cm. high. Many erect shoots arising from a woody *stem* close to base. These stems arise from a thick woody rootstock about 1·5 cm. in diameter. The plant is usually represented in the herbarium by single unbranched shoots but it is doubtful if it ever occurs thus. All have the appearance of having been broken off from a woody base. Shoots covered with whitish or bright yellow scaly pubescence which varies considerably in density. The shoots of some plants are practically glabrous or at the most have two lines of short pubescence. Shoots are terete or angular. *Internodes* variable, often only 3–4 mm. in small-leaved forms, but 1·5–6 cm. in larger-leaved ternate forms. *Stipules* small, trifid into narrowly triangular, setiform, yellowish segments about 1·5 mm. long. *Leaves* variable, paired or in whorls of three, the arrangement usually being constant on one plant, ovate-lanceolate to lanceolate, broadest near middle or at base, acute, deep green or pale yellow green; in small-leaved forms 7–10 mm. long, 3–5 mm. broad, in larger ternate-leaved forms about 1·5–2 cm. long and 4–11 mm. broad. The leaves of the small-leaved forms are usually entirely glabrous; those of the larger-leaved forms are either glabrous, glabrescent, or covered with short yellowish recumbent scaly hairs above, and have similar longer hairs on the veins below. The leaves of the type specimen are glabrous. Lateral nerves 3–4 on either side of the mid-vein. *Flowers* geminate in inflorescences which may be very condensed, few- to many-flowered heads 1–3 cm. across, or condensed heads with flowers arranged below in spikes for 4–5 cm. or even a group of inflorescences of the latter type arranged in an umbel. The flowers may be pale blue, pale pink or white. Pedicels 1–1·5 mm. long, somewhat woody and persistent. *Calyx tube* ovate, about 1·5 mm. long, pubescent. Calyx lobes 5, one lobe foliaceous ovate-lanceolate to linear-lanceolate acute, 6–7 mm. long × 1·5–2·5 mm. broad in larger-leaved forms, *c.* 3·5 mm. long × *c.* 1 mm. broad in the smaller-leaved forms, and rest of the lobes small and setiform less than 1 mm. long; or one large foliaceous lobe, one small foliaceous lobe and three minute lobes. Foliaceous lobes with three main veins and many lateral ones, glabrous or covered with scaly hairs or only hairy on margins. *Buds* usually with a few scattered scaly hairs, claviform, with limb indistinctly merged with tube. The tube develops after the lobes and stamens are almost mature. If buds of length 5 mm. are opened it is found that the lobes are 3·5–4·0 mm.

long and the tube only 1–1·5 mm. long. The anthers probably dehisce before the tube reaches its maximum length and possibly before the limb opens, i.e. the flowers may be cleistogamous. *Corolla tube* narrowly infundibuliform, much less filiform than in those species which have buds with limb expanded into a head and distinct from the tube, 4–5 mm. long, *c.* 0·3 mm. wide at base, 1 mm. wide near the limb. Throat densely hairy. Corolla lobes 5, lanceolate acute, 3·5–4·5 mm. long ± 0·7 mm. broad, with a few hairs at apex. *Stamens* 5, 4–5 mm. long, filaments hairy at base. Anthers scarcely 1 mm. long, yellow. Style 8–9 mm. long, stigma bifid, lobes filiform 1·5 mm. long. In buds of length 5 mm., i.e. those in which both corolla lobes and anthers are almost mature, the style is only 2·5 mm. long and the stigmas 1 mm. long. It is evident that the style elongates at the same time as the tube. *Fruit* ovoid, green or pale brown, about 2 mm. long, pubescent, but no mature fruits or seeds seen. The species is so far only known from eastern Southern Rhodesia.

SOUTHERN RHODESIA. Inyanga Mts., 6000–7000 ft., herb 8 in. high with bluish flowers, December 1899, *Cecil* 203 (K. TYPE). Pungwe Hills, Inyanga, 6000 ft., 30 January 1939, *Hopkins* 7176 (K. and S.). Inyanga, 6000 ft., low shrub about 2 ft. high with pale pink flowers, 8 November 1944, *Hopkins*, in Southern Rhodesia Govt. Herb. 13118 (K. and S.). Vumba, 5000 ft., 21 September 1939, *Hopkins*, Govt. Herb. 7078 (K. and S.). Vumba, in grass veld, 5000 ft., May 1946, *Greatrex*, Govt. Herb. 14936 (K. and S.). R. Mare, Inyanga, in open grassland, flowers pale mauve, 6100 ft., 21 October 1946, *Wild* 1555 (K.). By R. Pungwe, Inyanga, in grass, flowers pale blue, 6000 ft., 23 October 1946, *Wild* 1481 (K.). District Rhodes Estate, Inyanga, 19 December 1940, *Hopkins*, Govt. Herb. 7857 (K. and S.). Gazaland, Mount Pene, herb in open short grass veld, 7000 ft., 28 September 1906, *Swynnerton* 2007 (K.). Penhalonga District, in veld, 2 ft. high, with white flowers, 5000 ft., 11 December 1945, *Wild* 548 (K. and S.). Inyanga, on dry sides of clay gully, flowers mauve, 6000 ft., 21 October 1935, *Eyles* 8510 (K. and S.). Melsetter, flowers pale pink, 4000 ft., 24 February 1907, *Johnson* 170 (K.). Melsetter, 1 October 1919, *Walters* 2726 (K. and S.). Umtali, open country in short grass, erect plant with lavender flowers, 5200 ft., 16 February 1926, *Eyles* 1180 (K. and S.). Domboshawa, on granite rocks, woody perennial, 1 ft. high, flowers mauve, 7 March 1946, *Wild* 922 (S.). Same locality, in shallow-soiled declivity on granite, straggling shrub with minute pink-purple flowers, 5 October 1945, *Wild* 184 (S.). Umtali, Cloudlands, in open short grass veld, 5200 ft., flowers pale lavender, 16 November 1926, *Eyles* 5641 (S.). Stapleford, 12 and 19 June 1934, *Gilliland* 285 and 400 (S.). Inyanga, 22 January 1942, *Hopkins* 8652 (S.). Umtali, Vumba Mts., 6000 ft., perennial herb abundant in mountain grass veld, pink or mauve, 29 December 1946, *Fisher* 1120 (S.). Vumba, herb 1½ ft. high, flowers pink-mauve, 10 February 1942, *Craster*, Govt. Herb. 8714 (S.). Vumba, grassland, 15 May 1941, *Hopkins* 8052 (S.). Umtali Commonage, Bideford, abundant in disturbed veld, herb 2 ft. high, flowers pink, 30 January 1948, *Fisher* 1436 (S.). Inyanga, 'on way down to Hammers,' open grassland near rocks, mauve-flowered shrub 2 ft. high, 22 October 1946, *Rattray* 937 (S.). Inyanga, Troutbeck, in open grassland, flowers purple, a small-fruited form, fruits 1·25 × 1 mm., seeds oval, 1·25 × 0·75 mm., 2 March 1948, *Rattray*, 1437 (S.). Inyanga, inter Rhodes Estate et Pungwe, *c.* 5500 ft., 6 November 1930, *Fries, Norlindh & Weimarck* 2662. Inyanga, above Pungwe, *c.* 5400 ft., 18 December 1930, *id.* 3834. Inyanga, 3 km. occidentem versus a monte Inyangani, in vallicula, *c.* 6000 ft., 6 December 1930, *id.* 3523 (a leaf of one pair of leaves from this plant was distinctly bifurcate—a significant abnormality approaching a ternate arrangement). Inyanga, in Monte Inyangani, in campo fruticoso, *c.* 6700 ft., 7 December 1930, *id.* 3623.

In view of the great variability of this plant the writer was greatly tempted to consider it to include two species and a number of varieties. Although extreme forms are markedly distinct (e.g. *Eyles* 8510 and *Hopkins* 7078) they grade into one another. It is considered that it would be unwise to bestow many varietal names, until a careful ecological study of the species has been made, with a view to determining the nature of the variation. Accordingly, only one distinct variety has been named—*parvifolia*, but the chief types of variation are described below and specimens cited. All these agree in possessing the same floral structure, the hairy throat of the corolla being particularly distinctive. It is possible that the range of forms may be explained by postulating a hybrid swarm between var. *parvifolia* and form (*c*). These two forms are extremes and most of the specimens belong to them or have various intermediate characters.

(*a*) Typical form. Several erect shoots 15–30 cm. high from woody base. Leaves in whorls of three, larger 1·5–2·0 cm. long, 4–11 mm. broad, glabrous. Internodes 1·5–6·0 cm. long.—*Cecil* 203, *Johnson* 170 and *Wild* 548.

(*b*) Similar to typical form but robuster and shoots branched.—*Swynnerton* 2007.

(*c*) Both (*a*) and (*b*) exist in hairy forms, but there is clear intergrading between glabrous and hairy forms.—*Greatrex* 14936, *Hopkins* 7078. The former number has a remarkably large and peculiar terminal inflorescence. It is a distinct umbel of six or seven dense spikes so dense at the apices as to constitute heads.

(*d*) Between the above forms and those noted below are various intergrading forms with smaller narrower leaves or mixtures of variously sized leaves, in pairs, or whorls of three, or mixed. Internodes short.—*Hopkins* 7176, *Wild* 155.

(*e*) Several shoots from woody base, branched, somewhat angular and not very hairy. Internodes variable, some very short. Leaves paired, small, 7–10 mm. long, 3–5 mm. broad, glabrous. Foliaceous lobes of calyx much smaller than in typical form, and inflorescences small.—*Eyles* 8510.

O. inyangana N. E. Brown var. **parvifolia** var.nov., a typo differt *caulibus* brevibus usque 15 cm. procumbentibus striatis bifarie parce pilosis; *foliis* glabris acutis, lanceolatis vel ovato-lanceolatis, geminatis, subcoriaceis, ±1 cm. longis, 2–3 mm. latis.

SOUTHERN RHODESIA. Chimanimani Mountains, small creeping bush on rocks and ground, up to 6 in. high, flower white, 4 June 1948, *Munch* 87 (TYPE S.). Same locality, May 1947, *McCosh* 8 (S.). Same locality, 5000–7000 ft., 22 May 1942, *Weiste*, Govt. Herb. 9121 (S.).

The short axillary branches give a somewhat pseudo-verticillate appearance to the leaves. This form is related to *Eyles* 8510 (form *e*; *vide supra*) and also shows very clearly the connexion between *O. inyangana* and the other species placed close to *O. inyangana* in Fig. 2. The hairy throat clearly distinguishes it from any of these.

5. **Otiophora cupheoides** N. E. Brown in Hook. *Icon. Plant.* **15**, t. 1453 (1884). *Anthospermum calycophyllum* auct. non Sonder (1865). (Flower, Fig. 3*f*; bud, Fig. 4*n* and Fig. 3*e*.)

This species, one of the few which have been previously figured, is closely related in habit to some forms of *Otiophora inyangana*, but is readily distinguished by not having the throat of the corolla tube hairy.

Erect perennial undershrub with several branched stems 30–40 cm. high arising from a woody base. *Stems* greyish brown, somewhat angular, glabrous, irregularly striate, swollen at nodes, where the persistent stipules and leaf bases form little sheaths. Branches leafless below, often for 15 cm., glabrous where epidermis has peeled, but young portions clothed with yellowish bristly hairs. *Internodes* very variable, 1 mm. to 2 cm., but never uniformly short, always some longer ones towards apices of shoots. *Stipules* trifid, segments minute, ±1 mm. long. *Leaves* sessile, subcoriaceous, ovate-lanceolate and broadest near base, or elliptic-lanceolate broadest at middle, 0·6–1·5 cm. long × 0·2–0·7 cm. broad, entirely glabrous or with bristly hairs on midvein above and below. The leaf margins are often revolute. Lateral nerves *c.* 4 on either side of midvein. *Flowers* geminate, white, arranged in usually terminal inflorescences, which consist of a small head of flowers with further flowers arranged below in the form of a spike up to 5 cm. in length. Pedicels very short, ±1 mm. long, woody, persistent. *Calyx tube* ovate, *c.* 1 mm. long, covered with short hairs or tomentose. Calyx lobes 5, one, rarely two, foliaceous, lanceolate, 3·5–5 mm. long, 1–1·5 mm. broad, glabrous or with one or two odd bristly hairs on margin; rest of lobes minute, setiform, about 1 mm. long, sometimes with glands between them. *Buds* glabrous, claviform with limb indistinctly merged with tube, tube developing after lobes and with anthers practically of adult size (i.e. similar to *O. inyangana*), e.g. in buds of length 5 mm. the lobes are already of adult length. *Corolla tube* narrowly infundibuliform, similar to that of *O. inyangana*, 5–7 mm. long, 0·5–1 mm. wide at base and 1–2 mm. wide near the lobes, throat naked. Corolla lobes 5 (rarely 6), oblong-lanceolate, somewhat acute, 3·5–4·5 mm. long, scarcely 1 mm. broad, glabrous or with tiny scales at extreme apex. *Stamens* 5 (abnormally 6), about equalling the lobes, anthers small, less than 1 mm. long, pollen grains 30–33 μ in diameter, maturing before the buds open. Buds of length 5 mm. always contain anthers which have just begun to shed their pollen, whereas flowers which have opened have always been found to have completely empty anthers. Field work on this point is needed. Style 8–9 mm. long, stigma bifid, lobes filiform, *c.* 1 mm. long. *Capsule* pale yellowish brown, *c.* 2 mm. long, pubescent. Mature seeds not seen.

This species is so far only known from the Transvaal and Swaziland.

SWAZILAND. Hlalikulu: on grassy slopes, white flower, 4100 ft., *Stewart* 54 (K.).

TRANSVAAL. Houtbosch, *Rehmann* 5901 (K. TYPE). Berg Plateau, a ligneous procumbent white-flowered herb, *Mudd* s.n. (K.). Lydenburg Division, between Pilgrim's Rest and Sabie, *c.* 3500 ft., February 1920, *Rogers* 23687 (B.M.). Pietersburg Division, 'The Downs', no flowers present or fruit, *Rogers* 22076 (B.M.).

There are two well-marked varieties of this species.

O. cupheoides N. E. Brown, var. **macrosiphon** var.nov., ab *O. cupheoidi* typica corolla tubo usque 10–11 mm. longo differt (bud, Fig. 4*k*). This variety is quite distinct. The corolla tube is over twice the length of the foliaceous calyx lobe, whereas in typical *O. cupheoides* they are nearly equal in length. In the dry state it is possible to mistake the shape of the buds which are on the verge of opening (about 10 mm. long), but it is quite impossible to confuse this form with any of the other larger-flowered species. The length of the foliaceous calyx lobes and corolla lobes is the same as in typical *O. cupheoides*. Leaves glabrous. Flowers white.

TRANSVAAL. Saddleback Range, Barberton, amongst rocks on mountains, 5000 ft., December 1889, *Galpin* 729 (K. TYPE). Same locality, 4000 ft., 30 January 1889, *Thorncroft* 61. Same locality, 5000 ft., January 1928, *Thorncroft* 2183.

O. cupheoides N. E. Brown var. **hirsuta** (Bär) comb.nov. *O. hirsuta* Bär in *Vjschr. naturf. Ges. Zürich*, **68**, 435 (1923). *O. densiflora* Bär, loc. cit. 436.

The types of Bär's two species have been examined, and in the writer's opinion are merely forms of the same variety, in fact they may well have been part of the same plant. Both are *Junod* 856 and Bär separated out 856 and 856*a* for his descriptions. The Kew sheets merely bear the number 856. This plant seems to be no more than a hairy variety of *O. cupheoides*. The leaves are similar in shape and size to those of *O. cupheoides* but are covered with long, multicellular, whitish or yellowish, bristly hairs, those on the upper surface arising from small tubercles. The branches are densely covered with similar hairs but are glabrescent below. The foliaceous lobe of the calyx and the calyx tube are also covered with similar hairs. The buds and corolla lobes are often sparingly covered with long white hairs, but they may be glabrous. The corolla tube is slightly longer than it is in typical *O. cupheoides*, being 7–8·5 mm. long. The buds agree with those of *O. cupheoides* and var. *macrosiphon*, being intermediate in length between the two.

Bär's descriptions are accurate, although his interpretations were in the present writer's opinion much too narrow. Abridged statements of his descriptions are included here since many of the notes on general characters refer equally well to *O. cupheoides* as an aggregate:

O. hirsuta Bär. Undershrub, reaching 50–75 cm. in height, dichotomously much branched. *Young branches* densely covered with short hairs (subherbaceous during first year). New year's shoots 5–10 cm. long. *Inflorescence* often solitary and terminal, rarely with 1–2 lateral inflorescences running into it, short and dense during flowering time, lax and elongate after flowering, resembling a raceme but in truth cincinniform. *Leaves* decussate, lanceolate 1–1·5 cm. long × 0·5 cm. broad, suddenly attenuated towards the base, gradually towards the apex, very shortly petiolate, above obscurely greenish and rather shining, below paler and dull, densely pilose on both sides, the hairs on the upper sides of the laminae arising from tubercles, margin revolute, median nerve with two lateral nerves on either side. *Stipules* hidden by stem indumentum, small, segments 1 mm. long. *Flowers* very shortly pedicellate. *Calyx* densely and shortly pilose, four very narrow lobes 1 mm. long, fifth foliaceous 5 mm. long, canaliculate and glabrescent below, hairy above. *Corolla* almost three times as long as the foliaceous lobe of calyx (i.e. whole corolla), tube slender, throat somewhat infundibuliform, lobes half the length of the tube, linear, white, papillate on inner side, sparingly ciliate on outer side particularly towards the apex. Filaments 3 mm. long, anthers 1 mm. long ovoid. Style very slender, lobes of stigma 1·5 mm. long.

TRANSVAAL. Shilouvane, rocks at Marovougne and at Mamotsuiri, colour white, height 50–75 cm., January, *Junod* 856 (Zürich, TYPE, duplicates at Kew).

O. densiflora Bär. Undershrub up to 35 cm. high, much branched above. *Young branches* densely and shortly pilose, eventually becoming glabrous. *Leaves* opposite, broadly lanceolate or sub-rhombic, coriaceous, above obscurely green and somewhat shining, below pale and dull, margin somewhat revolute, densely pilose on both sides, median nerve with 2–3 arcuate lateral nerves on either side. *Inflorescence* terminal or lateral, subcapitate, becoming more or less elongate (up to 8 cm.). *Flowers* shortly pedunculate. *Calyx* densely pilose, sepals four short, fifth elongate and subfoliaceous 5 mm. long, hairy outside and glabrous inside. *Corolla* 10 mm. long, probably white, tube narrow, infundibuliform towards the throat, lobes narrow, linear, 2·5 mm. long, papillate inside, sparsely ciliate outside. *Stamens* inserted in throat, filaments 5 mm. long, filiform, anthers 1 mm. long, ovoid. Style filiform, ± 15 mm. long, stigmas 2 mm. long. *Fruit* 3 mm. long.

TRANSVAAL. Shilouvane, *Junod* 856*a* (Zürich, TYPE).

J. Bär suggests that the latter species is intermediate between *O. cupheoides* and *O. hirsuta* but denies that it is a hybrid. It will be seen that the above two descriptions carefully avoid directly contrasting the two so-called new species, and that different ways of saying the same thing are used in them. The writer has no hesitation in uniting them, and it is his opinion that they form a distinct variety of *O. cupheoides*. It is probable that others with a narrower concept of species will hold that it deserves specific distinction, but much more material and field work are required to settle the point.

6. **Otiophora pycnoclada** K. Schum. in Engl. *Jahrb.* **30**, 415 (1901). (Calyx, Fig. 3*d*.) This is a very distinct species, so far known only from one locality. It is chiefly characterized by its closely placed coriaceous leaves, which somewhat resemble the arrangement found in the shrubby *Veronica* species. It is clearly derived from the same ancestors as *O. cupheoides* and *O. calycophylla*, to which latter species it is related through *O. hebe*.

Perennial undershrub, reaching 30 cm. in height. Much branched from a woody base. *Shoots* grey-black, epidermis flaking off, glabrous, or pubescent in patches, leafless at base, covered with small sheaths formed at the nodes by persistent bases of stipules and leaves. *Stipules* fimbriate, ± pubescent at base, fimbriae setiform 2–3 mm. long. *Internodes* very short, mostly about 2 mm. long, but up to 4 mm. at apices of shoots. *Leaves* confined to tops of shoots, the sheaths below being the remnants of the previous years. Leaves sessile, oblong-lanceolate, 0·9–1·0 cm. long, 3–4 mm. broad, glabrous, coriaceous, rather shining dark green above, paler, less shining green below, very closely placed. *Flowers* violet, geminate in small terminal heads. *Calyx tube* ovoid-subglobose, just exceeding 1 mm. in diameter, sparingly covered with long white hairs, particularly on upper part. Calyx lobes 5, either one foliaceous and four small, or two foliaceous and three small, with several glands between the small lobes. Foliaceous lobes lanceolate, acute, glabrous or with few minute scales at apex, 5–6 mm. long, 1·5 mm. broad, smaller lobes setiform but not minute, ± hairy, and sometimes somewhat capitate, about 2 mm. in length. *Bud* with limb abruptly expanded into subcylindrical head quite distinct from the filiform tube, limb portion covered with long multicellular hairs, particularly on the veins of the lobes. *Corolla tube* filiform (certainly not infundibuliform as Schumann states in his description), only slightly broader at the top than in the middle, 6 mm. long, *c.* 0·5 mm. broad, lobes 5 lanceolate, 5 mm. long, 1 mm. broad, covered with long multicellular hairs particularly on the veins. *Stamens* 5, filaments 4 mm. long, anthers oval 1 mm. long attached near their middle. Style 8–9 mm. long, stigma bilobed, lobes filiform 2–3·5 mm. long. *Fruit* and seeds not seen. K. Schumann states the leaves to be 4–10 mm. long, 2–4 mm. broad below the middle, the stipules 1–1·5 mm. long, ovary 1 mm. long, sepals 2 or 6 mm. long, corolla (i.e. lobes and tube) 10 mm. long, corolla lobes 4 mm. long, and the style to be 10 mm. long.

TANGANYIKA. Ukinga Mts., in dry place with scattered blocks of rock on hillsides on Kipengere Ridge, 2700 m., flowering May 1899, *Goetze* 967 (Herb. Berlin, TYPE). Ukinga Mts., *Goetze* 965 (K. and B.M. duplicates from Herb. Berlin). Berlin material is not available so the type has not been seen, but it is probable that these two numbers are practically the same gathering.

7. **Otiophora hebe** sp.nov., ab *O. pycnoclada* K. Schum. foliis minoribus et corollae lobis minoribus glabris, ab *O. cupheoidi* N. E. Brown forma alabastrorum, ab *O. calycophylla* (Sond.) K. Schum. foliis coriaceis confertis differt.

Suffrutex erectus, lignosus, multiramosus. *Rami* asperi, irregulariter sulcati, ramuli laterales squamis pubescentibus vestiti et ad nodos vaginulis coartatis circumdati. *Stipulae* parvae, fimbriatae, persistentes, ramulis adpressae. *Internodia* brevissima, usque 1–1·5 mm. longa. *Folia* ad ramulorum lateralium apices spatio 3 cm. conferta, sessilia, oblongo-lanceolata, acuta, 8 mm. longa, 2 mm. lata, glabra, coriacea, supra nitida, subtus minus nitida, siccitate subtus rugulosa, utrinque nervis lateralibus vix distinctis. *Flores* geminati, in spicis brevibus terminalibus usque 2 cm. longis spiraliter dispositi; pedicelli brevissimi, sublignosi, persistentes. *Calycis tubus* 0·75 mm. longus, pubescens, superne in lobos 5 divisus; lobus foliaceus 1, lanceolatus, glaber, coriaceus, usque 3 mm. longus et 2 mm. latus, ceteri minuti vix distinguendi. *Alabaster* claviformis, tubo filiformi in caput ovatum abrupte expanso. *Corollae tubus* 4 mm. longus, filiformis, extra glaber, lobis 5 lanceolatis, sat obtusis, glabris, ad apices paullulo turgidis usque 2·5 mm. longis. *Stamina* 5 longe exserta, et stylus cum stigmate longe exsertus. Stigma bifidum, lobis filiformibus. Capsula et semina non visa.

TRANSVAAL. Blauwberg, on rocks above Nek and near top of Nek, 27 December 1923, *Pole Evans* 900 (K. TYPE), and *Pole Evans* 869.

This species is closely related in habit to *O. pycnoclada*, but differs in having smaller flowers, glabrous corolla lobes, slightly but uniformly smaller leaves, and shorter pubescence on calyx tube. It also differs in its calyx lobes, for though the foliaceous lobe is similar to that in *O. pycnoclada*, the non-foliaceous teeth are very much shorter and never have bulbous tips. It shows affinities with *O. cupheoides*, but the buds are very different in shape, and even closer affinities with *O. calycophylla*, but the leaves are arranged very differently. Further material is needed to fill in many of the lacunae in the above description.

8. **Otiophora pycnostachys** K. Schum. in Engl. *Pflanzenwelt Ost-Afrik.* C, 393 (1895). *O. caespitosa* S. Moore in *J. Bot., Lond.*, **63**, 146 (1925). (Bud, Fig. 4*g*; filament base, Fig. 4*m*; and seed, Fig. 4*q*.) This species is readily distinguished by its 'whorled' linear leaves, hairy bases of filaments and strict habit. S. Moore at the end of his description of *O. caespitosa* states that 'judging from the description this must resemble *O. pycnostachys* except that the leaves do not dry black. The laxly flowered spikes and nearly glabrous ovary and cocci are chief among the differences.' An examination of the types

has shown that the two are clearly conspecific and S. Moore's reference to lax spikes is confusing and incorrect.

Perennial herb or undershrub, from 15 cm. to nearly 1 m. high, one or several shoots arising from a woody base (S. Moore says densely caespitose, but his type is not; possibly the plants grow in tufts). *Shoots* erect, branched, terete or rather angular, with white hairs in two narrow lines on upper parts, glabrous below, brown. Lateral branches if present slender, often reaching nearly the same height as the main shoot. *Internodes* 1–10 cm. long, the largest occurring towards the tops of the shoots. *Stipules* pubescent, fimbriate into ±5 segments about 2 mm. long, the broad saccate base being persistent. *Leaves* apparently in whorls of 6–10, this pseudoverticillate effect being due to non-developed leafy branches in the axils of the two main stem leaves. This character readily distinguishes the species at a glance. Leaves linear-lanceolate, sessile, slightly coriaceous, somewhat revolute, 1–5 cm. long × 1–7 mm. broad, entirely glabrous or with a few short scaly hairs on margins and on midvein above. Lateral veins about four on either side of brownish midvein which is usually impressed above. *Flowers* geminate on minute pedicels, white, pinkish, or crimson, in heads or very compact subcylindrical spikes 2–4 cm. long, sometimes with a few flowers below the compact mass in a laxer arrangement. Besides the terminal inflorescence, there are frequently two lateral inflorescences at the apices of branches arising from the first internode below the terminal head. The whole inflorescence may thus appear to be a three-rayed umbel of spikes, but often when the lateral branches are very short the three inflorescences appear to be a single compact head. *Calyx tube* oblong-elongate, about 1·5 mm. long, densely hairy. Calyx lobes 5, one foliaceous, linear-lanceolate, acute, *c.* 5 mm. long × 0·5–1 mm. broad, hairy, particularly on margins; four small, setiform, hairy, and often somewhat dilated at apex. *Buds* with limb very abruptly expanded into a subcylindrical head, the bases of which form right angles with the sides of the filiform tube; limb with scattered white hairs particularly near apex. *Corolla tube* very filiform, 5–7 mm. long, *c.* 0·25 mm. broad, lobes lanceolate, 3·5–5·5 mm. long, *c.* 1 mm. broad, with scattered hairs exteriorly at apices. *Stamens* 5, exserted for 3·5–5 mm., filaments filiform with about 1 mm. close to the base somewhat dilated and covered with long white hairs. (Unless the corolla is carefully dissected it is easy to mistake these for hairs on the actual throat of the corolla.) Sometimes there may be a slight projection at the base of the filaments. Anthers ovate, bluish, *c.* 1 mm. long. Style 9–10 mm. long, very filiform, stigma bifid, lobes filiform, about 1 mm. long. *Capsule* elongate-ovoid, yellowish brown, striate, densely hairy or only slightly so, about 3 mm. long. Seeds oblong, often almost square at ends, just over 2 mm. long, 0·75 mm. broad, brownish (black when mature?), granulate, rather keeled for practically the whole length of the dorsal face.

Widely distributed in Northern Rhodesia and Tanganyika and also occurring in the Belgian Congo and Uganda, in boggy and swampy places.

BELGIAN CONGO. 'Marais', near L. Kivu: *Lejeune* 239 (B.).

UGANDA. L. Nabugabo (just to east of L. Victoria): in sphagnum bog, white flowers, 3750 ft., October 1932, *Eggeling* 582 (K.). L. Nabugabo, in fringing associations where short grass and coarser vegetation meet, one plant only, height 1 ft. 3 in., flowers white, 3900 ft., June 1937, *Chandler* 1708 (K.).

TANGANYIKA. 'Tropical East Africa', *Stuhlmann* (Herb. Berlin, TYPE, duplicate at K.). Iringa: Lupembe, banks of R. Ruhudje, January 1931, *Schlieben* 13 (K. and P.). Near Ifunda, *c.* 6000 ft., November 1928, *Haarer* 1600 (K.). Njombe, 2 January 1932, *Lynes* C.b. 75 m. and C.b. 75 q. (K.). Bukoba District: Bushasha Swamp, frequent on permanently inundated land, 14 August 1934, *Gillman* 94 (K.). Near Kaagyia in swampy place, 4000 ft., August 1931, *Haarer* 2106 (K.).

NORTHERN RHODESIA. Shiwa Ngandu, perennial herb up to 3 ft. tall, with flesh pink flowers. Common but scattered in the drier parts of moorland drainage peat bogs and associated with Cyperaceae, *Eriocaulon* and *Kyllinga*, 5500 ft., 19 July 1938

Greenway 5411 (K. and Amani). By R. Kasompa, west of Mwinilunga, in damp boggy ground, perennial, stems reddish, corolla white, anthers bluish, rest white, 31 October 1937, *Milne-Redhead* 3031 (K., duplicates at Brussels). Forty-four miles south of Abercorn, by stream, pinkish flowers, 5000 ft., 18 July 1930, *Hutchinson & Gillett* 3835 (K.). Luwingu, 4500 ft., *Jelf* 5 (B.M., Type of *O. caespitosa* S. Moore).

9. **Otiophora caerulea** (Hiern) Bullock in *Kew Bull.* **1933**, 471 (1933). *Pentanisia caerulea* Hiern, *Cat. Welw. African Plants*, pt. 2, p. 471 (1898). *Otiophora pulchella* K. Schum., ex De Wild., *Ann. Mus. Congo* Sér. IV, p. 230 (1903). *Borreria flavido-viridis* K. Schum. M.S. Herb. Berl. (Flower, Fig. 3*b*; calyx, Fig. 3*c*; bud, Fig. 4*e*; and seed, Fig. 4*r*.)

This is another distinct species which nevertheless is variable in certain characteristics, particularly the width of the leaves. It has a combination of well-marked characters which readily distinguish it from any of the other species. Some of its forms are a little like *Otiophora pycnostachys* (to which species it is related), but it lacks the hairy filament bases and hairy calyx tube of that species. *O. caerulea* has much the same habit as the caespitose small-flowered species of the genus.

Perennial herb, with 3–5 erect shoots, 15–45 cm. tall, arising from a woody rootstock, or with 3–5 erect shoots from each portion of a divided woody base. *Shoots* yellowish or purple brown, terete at base, compressed above, finely striate, usually with two narrow rows of short bristly hairs on opposite sides, or hairy all over at bases, unbranched in shorter plants or with numerous short opposite leafy branchlets arising in the axils of the leaves. *Internodes* 2–9 cm. long on main stem. *Stipules* small, broad at base, adnate to leaf bases, fimbriated above into 2–3 lanceolate or subulate segments 2–3 mm. long, somewhat pubescent. *Leaves* variable in width, sessile, linear, lanceolate, or elliptic-lanceolate, 3–4 cm. long, 2–9 mm. broad, bright green, often with a livid yellowish tinge in the dry state, quite glabrous, paired but occasionally appearing pseudoverticillate if axillary shoots remain undeveloped (this does not habitually occur, however, as it does in *O. pycnostachys*). Lateral veins brownish, 3–4 on either side of midvein. *Flowers* mauve on minute pedicels, geminate, in smallish compact heads, terminating main and axillary branches and branchlets, often giving the appearance of a single large head. *Calyx tube* ovoid or subglobose, glabrous (care must be taken not to mistake nearby stem hairs, and hairs on the minute calyx lobes, for hairs on the calyx tube). Calyx lobes 5, with one large foliaceous lobe and four short setiform ones, two large foliaceous lobes and three short setiform ones, or two large foliaceous lobes, one subfoliaceous lobe and two shortish setiform ones. Foliaceous lobes linear to lanceolate, acute, up to 10 mm. long × 1·5 mm. broad, glabrous or, in the case of subfoliaceous lobes, somewhat ciliate; setiform lobes 1·5–3 mm. long, somewhat bristly. *Buds* with limb abruptly expanded into an ovate or subcylindrical head, glabrous or slightly hairy. *Corolla tube* extremely filiform, from 7 to 12 mm. long, 0·25 mm. wide; lobes 5, lanceolate, 5–6 mm. long 0·75–1 mm. wide, glabrous or slightly hairy externally. *Stamens* 5, about equalling lobes, filaments glabrous. Style up to 18 mm. long, stigma bifid, lobes filiform up to 3 mm. long, somewhat spatulate at apices. *Capsule* subglobose, seeds dark brownish, subglobose, about 1·5 mm. diameter, granulated, with slight keel dorsally, and circular depression surrounding the hilum.

The species is widespread and common in upland grassland and at the edges of woods, etc., in tropical Africa.

BELGIAN CONGO. Mine de Luiswishi, February 1939, *Quarré* 5224 (B.). Near Baudouinville, 1926, *Robyns* 2079 (K.). Kundelungu, Upper Katanga Plateau, under trees, 13 March 1908, *Kässner* 2600 (K.). R. Lukifwa (?), open grassy plain, Upper Katanga, 24 May 1908, *Kässner* 2859 (K.). N'gano n'gano, Urundi, small blue-flowered plant abundant on high ground, 17 May 1920, *Shantz* 741 (K.). Mine de Vikasi, 17 March 1926, *Robyns* 1696 (K.). Route de Kasenga, 1926, *Robyns* 1781 (K.). Katanga, January 1900, native name 'Kampumboi', *Verdick* 320 (B. Type of *O. pulchella*).

TANGANYIKA. Mbosi, *c.* 5400 ft., November 1928, *Haarer* 1592 (K.). Bundali, Kalobosya, Rungwe District, 18 May 1912, *Stolz* 1280 (K.). Njombe, perennial herb

9 in. high with pale mauve flowers, in hillside grassland, 6000 ft., October 1931, *Staples* 211 (K.). Bulambya, Rungwe District, 15 March 1913, *Stolz* 1947 (K.). Njombe, common purple pasture weed, 10 December 1931, *Lynes* D.p. 114 (K.). North of L. Nyasa, 1880, *Thomson* (K.). Mt. Mbeya, in grassland, 9000 ft., June 1933, *Davies* M 23 (K.).

NYASALAND. Nyika Plateau, 6000–7000 ft., July 1896, *Whyte* 193 (K.). Between Mpata and the commencement of the Tanganyika Plateau, 2000–3000 ft., July 1896, *Whyte* s.n. (K.). Masuku Plateau, 6500–7000 ft., July 1896, *Whyte* (K.).

NORTHERN RHODESIA. Sinkabolo Dambo, Mwinilunga District, at edge of *Cryptosepalum* woodland on sand, perennial herb, shoots erect, stems bright cherry red, corolla tube mauve, limb whitish, flushed with violet, filaments violet, anthers yellow, 29 January 1938, *Milne-Redhead* 4388 (K. and duplicate at Brussels). Mwinilunga, river banks, plains and bush, grows almost anywhere, blue and white feathery flowers, 4500–5000 ft., January–March, *Marks* 77 (K.).

ANGOLA. Huila: along the road to Quilengues, R. Monino, in sparingly herbaceous somewhat shady places, in company with *Elephantopus*, in forest composed of *Protea* spp. and Myrtaceae, February 1860, *Welwitsch* 5314 (B.M. TYPE, duplicate at Kew). Bié-cuella District, in abandoned native plantations and short thicket-grown pasturage between R. Cutato and R. Cuchi as far as Munongue, *Gossweiler* 2437 (K.). Huila, 1800 m., *Dekindt* 1143 (K., duplicate from Herb. Berl. labelled *Borreria flavido-viridis* K. Schum., an MS. name). Benguela District, between rivulets Cuanza and Cului, December, *Gossweiler* 2932 (K.). Elende Mission, Cuma, plant up to 1 ft. in height, growing in thick clumps from a single root, flowers numerous, bright mauve, on the mountainside in poor stony soil, 4800 ft., 1940, *Faulkner* A. 319 (K.). Moxico District, by R. Mumbala in *Brachystegia* woodland, on sand, perennial herb, shoots erect, yellowish pubescent, corolla tube very thin, mauve, lobes lilac, filaments and style pale violet, 8 January 1938, *Milne-Redhead* 3991 (K.).

Although extreme forms are quite striking, the writer considers that the leaf variations in this plant do not deserve varietal names until it is clear how this factor is related to environmental conditions. The three forms which may be distinguished are as follows. Intermediate forms are plentiful.

(*a*) *Linear-leaved forms.* In these the leaves are only 2–3 mm. broad. Axillary branches present. *Robyns* 2079 may be taken as the type of this form.

(*b*) *Typical form.* Axillary branches present. Leaves 4–7 mm. wide, often large bushy plant, e.g. *Milne-Redhead* 4388.

(*c*) *Broad-leaved form.* Extremes of this are very distinctive. Stem usually unbranched, leaves suberect, elliptic lanceolate, 6–9 mm. broad. The leaves are all more or less uniform in size, since there are no axillary branchlets to bear any young leaves. It is this fact, coupled with the shortness of the plant and the width of the leaves, that makes this form distinctive, but intermediates occur. *Thomson*'s north of L. Nyasa specimen and *Staples* 211 are good examples. The form appears to be prevalent in Tanganyika.

10. **Otiophora multicaulis** sp.nov. ? *O. gracilis* K. Schum. ex De Wild. in *Ann. Mus. Congo Belge*, Bot. Sér. IV, ii, 154 (1913) nomen nudum.—Ab *O. caerulea* foliis et floribus minoribus differt.

Herba perennis. *Caules* 20–50, erecti, usque 13–17 cm. longi, e radice lignosa usque 5–8 mm. diametro exeuntes. Rami et ramuli rufescentes, teretes, graciles, pubescentia alba brevi recumbente obtecti. *Stipulae* parvae fimbriatae. *Internodia* 1–2 cm. longa. *Folia* parva, sessilia, ovato-lanceolata, 9–12 mm. longa 4·5 mm. lata, glabrescentia, supra squamis parvis paucis margine ornata, subtus costis parce pilosis. Nervi laterales utrinsecus 3–4 difficile distinguendi. *Flores* lilacini, geminati, in capitulis condensatis conferti, pedicelli brevissimi. *Calycis tubus* pubescentia alba indutus; calycis lobi 5, lobus foliaceus 1, 3–5 mm. longus 1–1·5 mm. latus, nunc ovato-lanceolatus nunc lanceolatus, minute reticulatus, supra pilis paucis squamosis ornatus, subtus glabrescens, ceteri minuti

pilosi. *Alabaster* claviformis, tubo filiformi in caput ovatum abrupte expanso, glaber vel squamulis minutis obtectus. *Corollae tubus* filiformis, usque 4 mm. longus, 0·25 mm. latus; lobi 4–5 anguste lanceolati usque 2·5 mm. longi, glabri vel minute externe squamosi. *Stamina* alba, 4–5, exserta, filamenta in fauce insidentia. Stylus longe exsertus. Stigma bifidum, lobis filiformibus. Capsula et semina non visa.

BELGIAN CONGO. ? Lubembe, 21 January 1908, *Kässner* 2349 (Herb. Berl., not seen). ? Plateau of Manika, October 1911, *Hock* s.n. (B.). See below.

NORTHERN RHODESIA. Mwinilunga District, south-west of Dobeka Bridge, on grey termite mound in open at edge of boggy grassland, 13 October 1937, *Milne-Redhead* 2739 (K. Type, duplicates at Brussels and Pretoria).

The name *Otiophora gracilis* was based on the Lubembe specimen, but K. Schumann apparently never published it. This sheet has not been seen and very probably is not now in existence. De Wildeman cites Hock's specimen under this manuscript name but gives no description. The Hock sheet has been examined, and though somewhat fragmentary is clearly related to *Milne-Redhead* 2739. It differs in having stems with hairs in two lines, glabrescent calyx tube and rather larger flowers, tube 6 mm. long and lobes 3–3·5 mm. long. It is, in fact, very like a dwarfed plant of *O. caerulea*, and the rootstock and stems show the signs of having been burnt. It seems unlikely, however, that the specimen is only an extreme state of *O. caerulea*. Further material is needed. The name *Otiophora gracilis* has therefore not been taken up.

This species is well characterized by the numerous graceful caespitose shoots arising from a thick woody rootstock. It shows no close affinities with any described species but agrees in habit with *O. caerulea* from which it is clearly distinguished by its very much smaller leaves and flowers.

11. **Otiophora latifolia** sp.nov. (Bud, Fig. 4*c*.) (See also Formae incertae sedis.)

Herba parva, perennis, usque 7–15 cm. alta. *Caules* usque 15, procumbentes vel subprocumbentes, ramosi vel non ramosi, e radice angusta sublignosa radiati. Caules pilis longis albis multi-cellulosis dense obtecti. *Stipulae* parvae fimbriatae, pilis caulis abditae. *Internodia* 1–3·5 cm. longa. *Folia* sessilia vel breviter petiolata, variabilia, plerumque ovata, nonnumquam orbiculata vel ovato-lanceolata, obtusa vel acuta, basi latissima, vel prope medium latissima et basin versus angustata, 10–19 mm. longa, 6–11 mm. lata, glabrescentia vel pilis longis multicellulosis obtecta, nervi laterales utrinsecus 4–5. *Flores* lilacini vel lilacino-caerulei, in capitulis condensatis terminalibus conferti, pedicelli brevissimi. *Calycis tubus* brevis usque 1 mm. longus, pilis longis multicellulosis obtectus; calycis lobi circiter 5, lobis foliaceis vel 1, vel 2 altero majore altero minore, forma et pubescentia sicut folia variabiles, ceteri minuti pilosi. *Alabaster* claviformis, tubo filiformi in caput ovatum abrupte expanso. *Corollae tubus* eximie filiformis usque 5–6 mm. longus, 0·25 mm. latus, lobi 4–5, ovato-lanceolati vel lanceolati usque 2–3 mm. longi, glabri vel squamis minutissimis albis obtecti. *Stamina* 4–5 per 2 mm. exserta, filamenta in fauce insidentia; stylus exsertus, stigma bifidum, lobis filiformibus usque 1·25 mm. longis. *Capsula* pallide fulva 2 mm. longa 1·5 mm. lata, pilosa, bilocularis. Semina ovato-depressa vel semiglobosa, cum foveis circa hilum ovatis vel rotundatis.

BELGIAN CONGO. Elisabethville, near Likasi Road, in sunny places, common, 3 February 1926, *von Hirschberg* 70 (K. Type). Near Kipushi mine, 25 March 1926, *Robyns* 1818 (K.).

TANGANYIKA. Njombe District, Madehani, strong smelling, 26 January 1914, *Stolz* 2466 (K.).

NORTHERN RHODESIA. Mufulira, procumbent on clay, leaves turn dull red with age, fruiting only, seeds hemispherical, *Eyles* 8158 (K. and S.). Mufulira, in *Brachystegia* woodland, 4000 ft., small tufts, stalks along the ground, brownish, hairy, flowers blue, 13 February 1949, *Cruse* 483 (K.). These two gatherings are identical, both have leaves which are intermediate in hairiness between var. *villosa* and typical material.

NYASALAND. Mt. Zomba and North Nyasa, 1896, *Whyte*, three unnumbered gatherings (K.). (Flowers rather larger than type.)

This species is variable and the study of further material may show that it is an aggregate of several closely related species. It is related to *O. parviflora* through var. *iringensis* of that species. Even in its more erect forms the present species may be readily distinguished from *O. parviflora* by the broadly ovate leaves and less caespitose habit. Several of the cited sheets of both *latifolia* and *parviflora* have in the past been named *O. pauciflora* Bak., but they are *totally* distinct from this species in habit, flowers, and seed. Two forms are sufficiently distinct to merit description as varieties.

O. latifolia Verdcourt var. **villosa** var.nov., ab *O. latifolia* typica ramis dense pilosis et foliis pilis longis multicellulosis obtectis differt.

NORTHERN RHODESIA. Kambole, south-west of L. Tanganyika, *c.* 5000 ft., 1896, *Nutt.* s.n. (K.). (Flowers rather larger than type.) Mwinilunga District, Kalenda plain, on grey termite hills among *Dissotis* and *Monotes* trees in drier ground between 'lateritic grasslands', corolla tube reddish mauve, filaments and style lilac, anthers yellow, 30 January 1938, *Milne-Redhead* 4410 (K. TYPE, duplicates at Brussels and Pretoria).

O. latifolia Verdcourt var. **bamendensis** var.nov., ab *O. latifolia* typica floribus minoribus, corollae tubo 4 mm. longo, lobis 1·5 mm. longis, alabastris et corollae lobis, pilis longis paucis externe obtectis et ramis dense hirsutis differt.

Leaves with few scattered hairs or glabrescent above, with long hairs on veins below. Foliaceous lobes of calyx broad and blunt, or narrow and more acute, with long bristly hairs beneath and at apex above, but with rest of upper surface glabrous or with small scales. Flowers predominantly tetramerous. A distinct variety.

BRITISH CAMEROONS. Bamenda, a rock plant and in grassland, flowers light mauve, 5000 ft., May 1931, *Maitland* 1445 (K. TYPE) and 1515 (K.).

12. **Otiophora parviflora** sp.nov., ab *O. caerulea* floribus minoribus et calycis tubo hirsuto, ab *O. multicauli* foliis majoribus et radice minore differt. (Flowers, Fig. 3*a*; bud, Fig. 4*d*.)

Herba annua vel perennis. *Caules* usque 20, erecti, circa 20 cm. alti, e radice lignosa usque 2–4 mm. diametro exeuntes. *Rami* et ramuli teretes, omnino dense pubescentes vel bifarie breviter pubescentes. *Stipulae* parvae fimbriatae. *Internodia* 2–3·5 cm. longa. *Folia* brevissima, petiolata, inferiora magis ovata 8–15 mm. longa × 5–7 mm. lata, supra breviter pilosa, subtus praesertim in costa pilis longis induta, sed indumentum variabile. Nervi laterales utrinsecus 3–4. *Flores* in capitulis condensatis conferti. *Calycis tubus* longe hirsutus; calycis lobi 5, lobo foliaceo 1, lobis 1–2 minoribus saepe additis, omnibus hirsutis, ovato-lanceolatis 4 mm. longis et 1·5 mm. latis, ceteri minuti. *Alabaster* pilosus, claviformis, tubo filiformi in caput ovatum abrupte expanso. *Corollae tubus* filiformis usque 3·5–5 mm. longus, lobi 4–5 usque 1·5–2·5 mm. longi, externe pilosi. *Stamina* 4–5 exserta, filamenta in fauce insidentia. Stylus exsertus, stigma bifidum lobis filiformibus usque 1·25 mm. longis. *Capsula* subglobosa, 2 mm. diametro, hirsuta; semina subglobosa, 1·25 mm. longa, 1 mm. lata, subtus depressa, supra convexa, reticulata et sat carinata, ad apicem subacuta, ad basin truncatula.

BELGIAN CONGO. Tonkoosji forest, Katanga, 19 January 1908, *Kässner* 2338 (K.).

TANGANYIKA. Rungwe District, Bundali, flower bright reddish lilac, 2000 m., 3 March 1914, *Stolz* 2574 (K.). North of L. Nyasa, 'Lower plateau', October 1880, *Thomson* (K.). These two are more glabrous than the type.

NORTHERN RHODESIA. Just north-east of Mufulira, in *Brachystegia* woodland, flowers white, 4000 ft., 18 January 1948, *Cruse* 161 (K. TYPE). Ditto, in fruit, 3 February 1949, *Cruse* 475 (K.).

O. parviflora Verdcourt var. **stolzii** var.nov., ab *O. parviflora* typica caulibus ramosioribus irregulariter et foliis lineari-lanceolatis vel linearibus usque 10–20 mm. longis × 1·3–3 mm. latis differt.

In this variety the foliaceous lobes or lobe of the calyx and the leaves are linear to linear-lanceolate. Stem with two lines of hairs. Buds and corolla lobes glabrous. Flowers rose. It shows affinities with *O. scabra* in habit and flower size but differs in inflorescence. Fruiting material is much desired.

TANGANYIKA. Njombe District, Madehani, 2000 m., 26 January 1914, *Stolz* 24677 (K. TYPE).

O. parviflora Verdcourt var. **iringensis** var.nov., ab *O. parviflora* typica caulibus paucis gracilibus, floribus violaceis, alabastris et corollae lobis glabris differt.

This form is allied to *O. latifolia* and more material is needed to decide its true affinities.

TANGANYIKA. Iringa Province, Msima Stock Farm, near Njombe, common on hillside grassland, 1932, *Emson* 372 (K. TYPE and Amani).

O. parviflora may be an aggregate of species but is best considered as one until very much more material has been collected and field observations have been made.

13. **Otiophora pauciflora** Baker in *J. Linn. Soc.* (*Bot.*) **20**, 170 (1883). (Bud, Fig. 4*f*; and seed, Fig. 4*o*.)

If the writer is correct in assuming that *O. burttii* is merely a variety of *O. pauciflora* then the distribution of this species is very peculiar. *O. pauciflora* was described from Madagascar, whereas *O. burttii* was described from the Virunga mountains in north-eastern Belgian Congo. Further material has been collected since, nearby, both in the Belgian Congo and in Uganda.

The species is readily distinguished by its long straggling stems, its moderately large flowers, and elongate seeds. It has been confused in the past with several of the caespitose small-flowered forms which occur on the African mainland but not apparently in Madagascar. It was this confusion which led to the description of *O. burttii* as an entirely new species, since this differed very much indeed from the mainland material wrongly called *O. pauciflora*. The writer's reasons for considering *O. burttii* a variety of *O. pauciflora* are as follows. A simple comparison of the types of the two would indicate at a preliminary glance that although the two are related they are quite distinct. In *O. burttii* the branching is more regular, but the chief differences are to be found in the leaves. Those of *O. burttii* are lanceolate, acute, revolute, rounded at the base, and minutely petiolate, whereas those of *O. pauciflora* are ovate, acute, less revolute, and are concavely narrowed at the base into a distinct petiole, about 1–2 and sometimes 4 mm. long. It is difficult to distinguish between petiole and the very narrow basal portion of the lamina. In *O. burttii* the flowers are pinkish, whereas those of *O. pauciflora* are usually white, the inflorescences have more flowers, the foliaceous lobe of calyx is usually single, and the corolla lobes are somewhat longer. The seeds of *O. burttii* are tapering-elongate and not elongate-rectangular as in *O. pauciflora* (but they vary in the latter). When, however, one examines the range of material from Madagascar and the few sheets from Belgian Congo and Uganda it becomes clear that *O. pauciflora* is extremely variable in leaf shape and flowers. Some Madagascar sheets (e.g. *Hildebrandt* 4053) come close to the type of *O. burttii*, and it is certain that if the plant which represents this type had been discovered in Madagascar it would have been called *O. pauciflora*. The additional Belgian Congo material does not match *O. burttii* exactly and helps to make the distinction even less clear. There is a possibility, of course, that this is an extreme instance of convergence and that the two forms are abundantly distinct both physiologically and ecologically, but such things cannot be decided by an examination of dry herbarium material.

Perennial herb, nearly always with 2–3 (possible more) long (maximum of 100 cm.), nearly always straggling, stems bearing numerous axillary branchlets, arising from a tapering woody rootstock, which is about 4–7 mm. diameter. *Stems* occasionally rooting at the nodes. Juvenile plants at the beginning of the first year are small, branched and erect (?) and presumably become long and straggling during this year. Stem and branches terete or somewhat angular, pale to deep brown, younger parts hairy, sometimes chiefly in two lines, lower parts glabrescent, striate, epidermis frequently flaking off. Axillary branches numerous, sometimes arising from one side only, or sometimes branch on one side quite long, whereas branch on opposite side of node is short and aborted. In the latter case the branches alternate in size, i.e. if at one node there is a long branch to the left and a short one to the right then at the nodes above and below the reverse is the case. *Internodes* variable, 0·5–6 cm. long, average about 2–3 cm. *Stipules* small, trifid to quinquefid into setiform segments, 2–4 mm. long. *Leaves* of the shape described above, 0·5–3·5 cm. long, 3–12 mm. broad, often quite discolorous, with short hairs above, and chiefly on veins below, or glabrescent. (The leaves of Baker's type are certainly not 'glabrous on both sides' as he states in his description.) Lateral nerves about 4 (rarely 6) on either side of the midvein. *Flowers* white or pale pink, in few- (2–10-) flowered, terminal heads, which may elongate into short spikes after flowering, usually with a few axillary flowers near the tops of the shoots as well. *Buds* with limb expanded into ovate or subcylindrical head, usually rather hairy particularly at apex. *Calyx tube* elongate, hairy or glabrous, about 1 mm. long, lobes 5, either three small and two large foliaceous ones, four small and one large foliaceous one, or three small, one medium foliaceous one and one large foliaceous one. The non-foliaceous ones are setiform, not uniform in size, 2–3 mm. long, and hairy. The foliaceous ones are ovate, acute, 4–5 mm. long, 2–2·5 mm. wide, ciliate round margins and the lamina is sparsely hairy or entirely glabrescent. *Corolla tube* filiform 6–12 mm. long, sometimes hairy; lobes 5, 3·5–5 mm. long about 1 mm. wide, usually with scattered hairs externally. *Stamens* 5, rather shorter than lobes. Style exserted for a distance equal to the lobes of the corolla, stigma bilobed, segments filiform, slightly flattened at apices, 1–1·5 mm. long. *Capsule* oblong elongate, 4 mm. long, 2 mm. wide, and 1 mm. thick, brown and hairy. Seeds black, reticulate, somewhat variable but always oblong-elongate, 2–3 mm. long, 0·75–1 mm. broad, dorsally with a central keel, and with an elongate depression ventrally, surrounding the hilum. The seeds are usually rather truncate at both ends but sometimes rather rounded, or slightly acute.

MADAGASCAR. Divisions as employed under *O. scabra*. Unless otherwise stated, the flowers are white, or no colour notes are given on the label. *Locality vague, undecipherable or not located on map*: Amboritra, dry steppes, 12 February 1889, *Scott Elliot* 2027 (K.). Ankaiziniana forest, 1100 m., 19 April 1923, *Decary* 1976 (P.). Central Madagascar, *Baron* 1009 and 444 (K. and P.) and 1118 (K.). Ivohimanitra? forest, November 1894, *Forsyth Major* 13 and 72 (K.). Mt. Ankaroba, south-east of L. Alastra, gneiss outcrop in forest, 1200–1400 m., narrow-leaved form, rooting at nodes, seeds typical, October 1937, *Humbert* 17468 (P.). No locality, 9 November 1877, *Rutenberg* (P.). Wald de Amb - - - - lato, 6 December 1877, *Rutenberg* (P.). Sahanaly?, 14 March 1889, *Cazat* 1228 (P.). Analamohita forest, 900 m., damp wood, sprawling on the ground and rooting at the nodes, 1907, *Perrier* 3618 (P.). Forest of Ambamahito, massif of Marrung - - - t? amongst lichens, 1000 ft., leaves narrower, flowers smaller and seeds a little more elongate than typically, *Perrier* 3804 (P.). Massif of Andohapelo (south-east), valley of Ranohela, forest on gneiss laterite, 1200–1800 m., 18 October 1928, *Humbert* 6099 (P.). ANALALAVA AND VOHÉMAR: Massif of Tsaratanana and high valley of Sambirano, shady forest on siliceous soil, quartzite rocks, 1400–1800 m., small narrow-leaved form and flowers rather small, but seeds typical, November 1937, *Humbert* 18196 (P.). TANANARIVE: Imerina, in dry soil, *Lyall* 305 (K. TYPE). Andrangaloaka, near Tananarive, a ground creeper with white or pale yellow flowers, *Parker* (K.). Same locality, November 1880 and May 1881, *Hildebrandt* 3665 and 4053 (K., P. and V.). Forest of Ambohiby, rocks, 1600 m., 31 January 1933, *Leandri* 776 (P.). Tananarive, covered places, July 1907, *D'Alleizette* 555 (P.). Mantosoa, border of high plateaux, prairie, 1400–1500 m., flowers rosy white, 12 November 1927, *Decary* 6081 (P.). Ditto, humid places, same date, *Dec.* 6101 (P.). South of Moramanga, humid places, very pale rose flowers, 14 February 1930, *Dec.* 7095 (P.). Ditto, forest clearing, 20 February 1930, *Dec.* 7118 (P.). Tampoketsa to the north of Ankazobe, wet rocky places, small narrow-leaved form rooting at the nodes, flowers rose-white, 12 March 1930, *Dec.* 7462 (P.). Forest of Ambohilantely to north of Ankazobe, flowers rose, a small very narrow-leaved form, which as preserved bears a slight resemblance to forms of *O. pycnostachys*, 12 March 1930, *Dec.* 7445 (P.). Ankaratra, gneiss rocks, 2000 m., stems sprawling, roots orange yellow, flowers white or lilac, 1914, *Perrier* 3526 (P.). Basin of R. Mangoro, on site of cleared forest, gneiss, 2000 m., plant sprawling on the ground, September 1911, *Perrier* 3902 (P.). Tampoketsa to the north of Ankazobe, forest of Ambohilantely and others nearby, 1600 m., October 1933, *Humbert* 11059 (P.). District of Manyakandriana, in the forest near Ambatolaona, 1400 m., flowers rose-white, elongated leaves, 11 November 1912, *Viguier & Humbert* 1199 (P.). Mantasua, 1889, *Myre de Vilers* (P.). District Manyakandriana, Angavo, 1922–3, *Waterlot* 681, 666 and 588 (P.). Marisana under trees, lanceolate leaves, July 1907, *D'Alleizette* 550 (P.). AMBOSITRA: Ambohimitombo forest (tanala?), 1350–1440 m., November 1894–January 1895, *Forsyth Major* 409 and 389 (K.). Massif of Ankaratra, eastern side of Tsiafajavona, remains of forest, 1700–2000 m., 15 July 1928, *Humbert* 4547 (P.). Same district, forest of Manjakatompo and its borders, October 1933, *Humbert* 11173 (P.). Mt. Vatomavy near Ambositra, siliceous rocks, 1500–1870 m., 23 July 1928, *Humbert* 4752 (P.). Near Ambatofinandrahana, 1600–1800 m., humid places, flowers rosy-white, 16 February 1938, *Decary* 12983 (P.). FIANARANTSOA: Andringitra Mts., amongst grass and shrubs on slopes, 8000–9000 ft., January 1889, *Scott Elliot* 1837 (? but states Imerina on label), (P.). Massif of Andringitra, Iratsy, valley of the Riambara and Antsifotra and nearby mountains, 2000–2500 m., November 1924, *Humbert* 3707 (P.). Basin of Matitanana, high valley of the Rienana forests, 1000–1400 m., flowers very pale lilac, November 1924, *Humbert* 3553 (P.). VANGAINDRANO: basin of the R. Itomampy south-east of Mt. Papanya close to Befotaka, siliceous rocks, 1300–1700 m., 2 December 1928, *Humbert, Decary & Swingle* 6905 (P.). Mt. Itrafanaomby (Ankazondrano), gneiss rocks and lateritic clay on slopes, 1600–1963 m., December 1933, *Humbert* 13474 (P.).

Variation in O. pauciflora. The writer has been greatly tempted to split the species into a number of distinct varieties, or even species, and it is possible to pick three sheets, say, out of those cited, which it is indeed difficult at a cursory glance to believe are not all quite distinct species. The examination of a large amount of material has shown, however, that it would be very difficult to draw the line between these varieties, and that it is better to admit that the species is a very variable one. For instance, *Baron* 1009 is extremely different from the large-leaved forms, and the author was going to make it the type of a variety having small, ovate, petiolate leaves only 5–6 mm. long and 3–4 mm. broad, but it is only at the extreme end of a range of variation. Many sheets have large and small leaves intermingled. The variation in the leaf-shape may be summarized:

(1) Ovate-leaved type with lamina narrowed into a distinct petiole. The latter often appear longer than they actually are, since they are barely distinguishable from the very narrow bases of laminae. The leaves are broadest near the middle and vary from 0·5 to 2·0 cm. long and 3 to 8 mm. broad.

(2) Elliptic-lanceolate-leaved type. There is every gradation between this type and the last. Since the leaves are more elongate the narrowing into the petiole does not appear so striking. Leaves broadest at middle, 1–3 cm. long, 2·5–10 m. broad. *Hildebrandt* 4053 and *Viguier & Humbert* 1199 are examples. The petiole varies a good deal and there are distinctive forms in which the leaves are narrow lanceolate and the petiole short, e.g. *Decary* 7445. It is this type which shows the relationship to var. *burttii*.

It is not unusual to get mixtures of these types, and since the degree of straggling varies a great deal there is no end to the forms which may be found. One sheet, however, seems to merit a varietal name since intermediates are rare.

O. pauciflora var. **ovata** var.nov., ab *O. pauciflora* typica foliis basi latissimis et petiolis brevissimis differt.

Stem hairy. Leaves 8–13 mm. long, 6–10 mm. broad, ovate, mostly broadest very close to base, some being subcordate, very abruptly narrowed into very short petiole 1 mm. long. The seeds and flowers are quite the same as those of the typical material.

MADAGASCAR. Tananarive District. Analamozoatra, borders of road, 800 m., *Perrier* 3669 bis (P. TYPE). Despite the distinctive appearance *some* of the leaves are not very different from typical *O. pauciflora*. *D'Alleizette* 555 is an intermediate between the variety and the typical material.

O. pauciflora var. **burtti** (Milne-Redhead) comb.nov., *O. burttii* Milne-Redhead in *Bull. Soc. Bot. Brux.* **18**, 103 (1946). (Seed, Fig. 4*p*.)

The leaf differences have already been discussed at the beginning of the section on this species. The inflorescence contains more flowers, and if a spike results after flowering it is longer and denser in some of the specimens. The buds are similar in shape but hairier. The corolla tube is occasionally hairy. The foliaceous calyx lobes are less ovate than in *O. pauciflora*. The seeds are elongate but rather smaller and distinctly tapering, 1·5–2 mm. long, 0·5 mm. broad or a trifle broader. The capsules are a little smaller, 2·5–3 mm. long.

BELGIAN CONGO. Mashiga Pass, between Mts. Sabinio and Vissoke, trailing over tussocks in swamp, a pale lilac-flowered herb seen only in this one place, 2100–2200 m., 14 December 1930, *Burtt* 2993 (K. TYPE). Kanzibi, in marshes in mountains to west of L. Kivu, flowers rose violet, 2200 m., 1929, *Humbert* 7510 (K.). Kahugi, Tshibinda, *Scaetta* 1387 (K.). Mukarumbi, 1926, *Robyns* 2381 (K.). These three latter sheets had been wrongly named *Anthospermum lanceolatum*.

UGANDA. Mushongero, L. Mutanda, Kigezi (some 10 miles from type locality), herb with pinkish white flowers, November 1940, *Eggeling* 4235 (K.). Bukimbiri, Bufumbira, Kigezi, in short grassland, altitude 6000 ft., herb 2 ft. high, flowers pale pink, October 1947, *Purseglove* 2502 (K.).

FORMAE INCERTAE SEDIS

14. **Otiophora sp**. The writer has been unable to place the following specimen, and the material is too scrappy to describe as new, but a brief description is included here.

Herb, a single shoot measuring 20 cm. high, is preserved, leafless for the basal 7 cm. Stem somewhat angular, hairy in two lines. Internodes 0·5–2 cm. long. Stipules small, ± quadrifid, segments narrowly triangular, *c.* 1 mm. long. Leaves ovate-lanceolate, acute at apex, sessile, rounded at the base, ± 2 cm. long × 0·6 cm. broad, glabrous, somewhat shining deep green and reticulate above, duller paler green below. Some of the upper leaves have ciliate margins and a few hairs on veins below. Flowers in compact heads. Calyx tube pubescent, ovoid, almost 1 mm. long, lobes 5, one foliaceous, lanceolate, acute, 5 mm. long × 1·2 mm. broad, shining and reticulate above, somewhat ciliate round margin, surfaces sparingly covered with tiny white scales, rest of lobes reduced to small teeth. Buds with limb abruptly expanded into an ovoid head, both limb and tube sparingly covered with minute scales which persist when the corolla opens. Corolla tube ± 5 mm. long; lobes 5, *c.* 4 mm. long, probably somewhat turgid or fleshy in living state. Throat and base of filaments glabrous. Stigma lobes ± 2 mm. long. Ovules erect.

TRANSVAAL. East Zoutpansberg, grassy place north of Pepiti, 3800 ft., 21 August 1930, *Hutchinson & Gillett* 4367 (K.).

Further material will almost certainly show that this form represents a new species allied to *O. inyangana*, to *O. multicaulis* and *O. caerulea*, but quite distinct in flowers and foliage. It comes near *O. multicaulis* in the key.

15. **Otiophora villicaulis** Mildbraed in *Notizblatt Bot. Mus. Berl.* **15**, 637 (1941). From the description this species would appear to be related to *O. latifolia* Verdcourt, but in the absence of a specimen the exact relationships cannot be decided. The following is a translation of the description.

Perennial herb with obtusely quadrangular branched decumbent stems, rather densely covered with pale yellow hairs, internodes 2–4 cm. long. Leaves subsessile, exactly ovate, obtuse, 15–20 mm. long, 10–15 mm. broad, almost glabrous above; below with 4–5 arcuate ascending nerves on either side of the midvein, crisply pilose towards the base. Flowers at apices of branches, in close capitate cymes. Ovary globose, pilose, one ovule in each loculus. One of the calyx segments greatly enlarged, foliaceous, oblong-lanceolate obtuse, 4·5 mm. long, 1·5 mm. broad [the 4·5 cm. and 1·5 cm. of the original descriptio are surely mistakes], rest of segments small, subulate but soft, unequal. Corolla (*ex dr* material) pale lilac, tube very narrow, 6 mm. long, lobes 4, elliptic-oblong, about 3 mm long and 1 mm. broad. Filaments inserted at the margin of the tube, 1·5 mm. long Anthers scarcely 1 mm. long, oval-oblong in outline. Style bifid, branches 2 mm. long.

TANGANYIKA. Matengo Highlands, W.S.W. of Songea, on roads, paths an bare places in bush near Ugano, 1400–1600 m., flowering, 28 January 1936, *Zerny* 37 (TYPE, destroyed). This species, Mildbraed says, is well distinguished by the floccos pubescence of the stem and by the broad leaves.

The type formerly at Berlin was burnt during the war. Prof. Mildbraed thought tha the Vienna Herbarium (from whence Zerny's specimens were sent in the first instance had a duplicate, but the authorities of that institution have informed the writer tha there does not appear to be one. This being so it is highly unlikely that there are any a all, but the author has refrained from identifying his *O. latifolia* with this species, since although it is quite probable that they are the same, a duplicate may turn up or th species may be re-collected from the type locality and prove that the two are quit distinct.

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Some Cornish Rubi. By F. Rilstone, A.L.S.

[Read 24 November 1949]

The *Rubus* flora of that part of the south-western peninsula lying west of Dartmoor differs considerably from that of the remainder of south-west England; its affinities seem to be more with Pembrokeshire and Carmarthenshire. The following characteristic brambles of the region appear to be distinct species and are here described and named. It seems fitting to associate with them the names of four former Cornish botanists who collected Rubi—F. H. Davey, E. Thurston, W. Tresidder and C. C. Vigurs—and also Rev. H. J. Riddelsdell who was greatly interested in the brambles of the south-west. Of nine of these species I have been able to verify the natural occurrence of seedlings true to type, largely because they grew where I was able to keep them under almost continuous observation. With the other three, *R. peninsulae*, *R. coombensis* and *R. carnkiefensis*, I had not the same opportunity.

1. **Rubus Daveyi**, sp.nov. *Turio* arcuato-decumbens, obsolete angulatus, glaber, subfuscus, aculeis longis paucis reclinatis armatus. *Folia* plerumque 5-nata. Foliola supra strigosa, subtus leviter pilosa viridia. Foliolum terminale oblongo-ellipticum, cordatum, abrupte acuminato-cuspidatum, longe petiolulatum. *Inflorescentia* laxe pyramidalis, inferne foliosa, flexuosa, tenuiter pilosa, rubro-purpurea, aculeis sparsis armata. *Sepala* dense tomentosa, breviter acuminata, fructu reflexa. *Petala* ampla, violaceo-rosea. *Stamina* longa stylos superantia.

Stem rather low-arching, bluntly angled to roundish (or sometimes rather furrowed in the upper part) with the angles never very noticeable to the touch, smooth and conspicuously glossy, red or purplish to brownish olive above, pale green underneath. Prickles rather few, often long, straight, slightly declining, usually bright crimson at base with the sharp slender point pale yellow or straw-coloured. Stem *leaves* 3–5-nate, mostly 5-nate, petiole often standing off at a right angle or even deflexed, with a few curved prickles. Leaflets occasionally plicate but typically smooth, convex, dark or yellowish green. Petioles and petiolules downy or slightly hairy. Terminal leaflet convex, typically elliptic-oblong or slightly obovate, cordate, abruptly cuspidate, with a stalk half or more of its own length and with rather shallow simple toothing, thinly strigose above, thinly hairy on the veins beneath (to the naked eye both surfaces appear glabrous), all leaflets with prominent veins beneath. *Panicle* when well developed pyramidal and then leafy below, often with 5-nate leaves like those of the stem; but small cylindrical panicles are sometimes altogether ultra-axillary. Rachis wavy, slightly downy, with very few hooked prickles, generally quite unarmed in the upper part, reddish purple. *Sepals* thickly softly felted, shortly acuminate, rather strongly reflexed in fruit. Flowers large, showy; petals spreading well apart, obovate, of a striking violet-pink colour. *Stamens* long, exceeding the styles, the filaments white above and pink below. *Styles* spreading, greenish to flesh-coloured. Fruit large, sweet, sometimes thimble-shaped.

This is *R. nemoralis* of Davey's *Flora of Cornwall*, and is locally plentiful throughout the county. It is nearest to *R. Silurum* (Ley) Watson, but has a very different terminal leaflet (oblong-obovate or oblong-elliptic, cordate, cuspidate, instead of subrotund or broadly elliptic), and differs also in the scanty armature of the panicle, the usually convex leaflets, the different flowers, etc.

Exsiccata: Herb. Rilstone no. 4900, Lambourne, July 1949 (typus); no. 690, near Perranzabuloe Church, August 1930; no. 535, between Launceston and Whitstone, August 1927, Thurston and Rilstone.

2. **Rubus cornubiensis** sp.nov. (*R. nemoralis* var. *cornubiensis* Rog. & Ridd., *J. Bot., Lond.*, 1925, p. 14). *Turio* arcuatus, fere glaber, aculeis reclinatis vel curvatis armatus. *Folia* 5-nata, digitata vel pedata, ampla et plana vel parva et plicata. Foliola supra

strigosa subtus plerumque albo-tomentosa. Foliolum terminale obovatum, cordatum, breviter acuminatum vel truncato-cuspidatum. *Inflorescentia* pyramidalis vel anguste oblonga. Rachis flexuosa tomentosa laxe pilosa, glandulis stipitatis paucis et aculeis tenuibus instructa. *Sepala* tomentosa pilosa, fructu reflexa. *Petala* rosea, late obovata cuneata vel rotundata. *Stamina* alba stylos superantia.

Stem bluntly angled, nearly glabrous, purple above. Prickles often crowded and patent at base of stem, elsewhere fewer and somewhat declining or slightly curved, slender from longish base. *Leaves* 5-nate, pedate or digitate. Leaflets often small and plicate and heavily white-felted beneath in full sun and in dry spots, but larger, smoothly convex and less, or not, felted in moist shady places; then sometimes very large and lacking felt. Toothing rather fine to moderately coarse with apiculate points, compound towards the apex of the leaf. Terminal leaflet obovate cordate (occasionally with entire base), shortly acuminate to abruptly cuspidate-acuminate on a petiolule about one-third of its own length. Strongly truncate leaflets are often almost quadrate. Well-grown *panicles* somewhat pyramidal, leafy below, with a rather narrow almost cylindrical ultra-axillary part. The smaller bushes with highly plicate leaves usually have small narrowly cylindrical panicles. Rachis flexuose with close felt, some short spreading hair and a few, mostly short, stalked glands and fairly many slender patent to declining prickles. *Sepals* triangular ovate with a fairly long apiculus, hairy and felted, reflexed in fruit. Flowers showy and cup-shaped. *Petals* pink, roundish or broadly obovate cuneate, hairy on the back, ascending and contiguous. *Stamens* white, much longer than the green styles. Fruit large, drupelets glabrous.

Exsiccata: Herb. Rilstone no. 4901, Lambourne, July 1949 (typus); Par, East Cornwall, July 1924, H. J. Riddelsdell, ref. no. 904.

A frequent plant in most parts of the county from the Lynher valley westwards, but perhaps chiefly on the higher ground. Mr W. Watson refers it to *R. bifrons* Vest but, though the plate in Sudre's *Rubi Europae* (T. LXXXII) shows a plant with something of the look of *R. cornubiensis*, I can see no close similarity; nowhere, for instance, is there any suggestion of the abruptly cuspidate leaf point so characteristic of the Cornish plant. Moreover, Focke's Drachenfels gathering of *R. bifrons* (1875) shows somewhat erratically branched panicles with rachis prickles declining or curved which do not at all match Sudre's drawing, and the photographs of *R. bifrons* in Focke's *Species Ruborum* are quite unlike any form of *R. cornubiensis*. In addition, the sheets I have seen sent out by continental botanists as *R. bifrons* in the years prior to 1939 are also quite different from *R. cornubiensis*.

3. **Rubus Tresidderi**, sp.nov. *Turio* fuscus, sulcatus, fere glaber. Aculei parum inaequales, parvi, plerumque ad angulos dispositi. *Folia* 5-nata digitata vel pedata. Foliola lata, supra strigosa, subtus pilosa et leviter tomentosa, subsimpliciter serrata, plicata. Foliolum terminale cordatum, rotundatum vel ellipticum, acuminato-cuspidatum. *Inflorescentia* pyramidalis, foliosa. Rachis valde flexuosa, laxe pilosa, aculeis debilibus instructa. *Sepala* ovata, fructu reflexa. *Petala* obovata purpureo-rosea. *Stamina* stylos valde superantia.

Stem low-arching, robust, brownish purple, furrowed, with very few adpressed hairs and with rather short and weak, somewhat unequal prickles, almost confined to the angles of the stem, patent or slightly declining or slightly curved. *Leaves* 5-nate, digitate or pedate, with petioles and petiolules somewhat hairy and rather prickly, the prickles usually only slightly curved. Leaflets broad, plicate, somewhat strigose above and with some hair and felt beneath. Terminal leaflet cordate, roundish or broadly elliptic with a short cuspidate-acuminate point. *Panicle* when well developed pyramidal with very wavy rachis, 3-nate leaves below and mostly simple ones above. Rachis and its branches with loose-spreading hair but little felt, and with rather weak falcate or straight slender prickles. *Sepals* triangular ovate with fairly long point, hairy and felted, reflexed in fruit. *Petals* fairly large, rich purplish pink fading to paler pink, rather broadly

obovate, somewhat crumpled. Purple-based *stamens* much longer than the greenish styles.

Exsiccata: Herb. Rilstone no. 4902, Lambourne, July 1949 (typus); no. 2603, Lambourne, 24 July 1946.

A frequent plant in the area about Lambourne and Perranzabuloe Church. Its affinities appear to be with *R. cornubiensis* and *R. dumnoniensis* Bab., but it differs from both in the armature, flower colour, form of panicle with its strongly flexuous rachis, and the shape of the terminal leaflet.

4. **Rubus lamburnensis**, sp.nov. *Turio* sulcatus, tomentosus, laxe pilosus. Aculei reclinati, ad angulos dispositi. *Folia* lata, valde plicata, subtus saepe albo-tomentosa. Petioli sulcati. Foliolum terminale cordatum, late ellipticum vel rotundato-obovatum. *Inflorescentia* cylindrata. *Sepala* post anthesin patula. *Stamina* alba stylos superantia.

Stem dull purplish above with pronounced shallow furrows and prominent rounded ridges along the angles, with a good deal of stellate pubescence, often disappearing from the older stems, and usually much appressed or spreading white hair. Prickles mostly confined to the angles, often irregularly spaced, mostly straight and declining with long slender points or, on the more robust stems, stouter and shorter. Petioles distinctly furrowed, with rather few hooked prickles and loosely appressed hair. Mature *leaves* with leaflets broad and plicate, white-felted or greenish beneath with prominent veins. Terminal leaflet broadly elliptic, roundish-ovate or roundish-obovate, cordate, cuspidate-acuminate, 2–3 times as long as its stalk, coarsely often nearly simply mucronate serrate. *Panicle* cylindrical or somewhat pyramidal usually with stout, rather long, patent peduncles above and ascending branches below, leafy with usually 3-nate to simple leaves. Rachis stout and rather wavy clothed with dirty yellowish or whitish grey hair and felt, and with declining prickles, often few and slender in the upper part. *Sepals* broad, very concave, apiculate, with close whitish felt and short hair, patent with upturned tip at fall of petal, often soon subpatent or loosely reflexed. *Petals* creamy white, or at first pinkish, crumpled, concave and upturned, of moderate size, broadly to narrowly elliptic with short claw, hairy on the back. *Stamens* white, longer than styles.

Exsiccata: Herb. Rilstone no. 4903, Lambourne, July 1949 (typus); no. 915, Lambourne Hill, August 1935.

A common plant about Lambourne and Perranzabuloe Church and within a radius of several miles from thence. A gathering was distributed from Ventongimps through the British Botanical Exchange Club in 1938 and was there named *R. propinquus* P. J. Muell. But the sheets of that species in Herb. Mueller (no. 1316, coll. Chaboisseau, Pindray, 23 June and 16 August 1861) show a plant which is quite distinct from this. In that, the stem leaves show a terminal leaflet uniformly of a beautifully regular, rather narrowly elliptical shape, with mostly shallow toothing and with base entire or emarginate, the proportion of length to width being 11 : 8. In *R. lamburnensis* the terminal leaflet on mature leaves is broad and cordate, with the width nearly as great as the length. The panicles of authentic *R. propinquus* do not show in the upper part the long rigidly patent peduncles characteristic of the Cornish plant. Moreover, the collector's notes state that the petiole of *R. propinquus* is plane on the upper face with at most only a narrow line to indicate a furrow, while that of *R. lamburnensis* bears a distinct broad shallow furrow, and the petals (of *R. propinquus*) are subrotundate and pink (rosea), while the sepals are reflexed immediately on the fall of the petals. Here again, curiously enough, Sudre's drawing of *R. propinquus* shows rather more resemblance to the Cornish plant.

5. **Rubus Riddelsdelli**, sp.nov. *Turio* obtusangulus, pilosus, faciebus planis vel sulcatis. Aculei longi, recti, perum inaequales, plerumque ad angulos dispositi. *Folia* plerumque 5-nata, digitata, plicata, subtus tomentosa vel pilosa. Foliolum terminale ellipticum emarginatum acuminatum. *Inflorescentia* cylindrata vel pyramidalis, supra saepe densa, inferne interrupta foliosa, foliis saepe longe attenuatis. Rachis flexuosa pilosa tomentosa, plerumque eglandulosa, aculeis longis reclinatis armata. *Sepala* fructu

reflexa. *Petala* sat anguste elliptica, alba vel pallide rosea. *Stamina* alba stylos valde superantia.

Stem purplish red in exposure, rather bluntly angled, somewhat furrowed in the upper part, with numerous somewhat unequal strong-based patent prickles with long slender points, not quite confined to the angles. Stem considerably but not densely hairy, with single or clustered hairs adpressed or spreading and only an occasional trace of felt. *Leaves* mostly 5-nate digitate with numerous hooked prickles on the petioles and usually with prickles on the back of the midrib in all leaflets. Leaflets mostly plicate with veins prominent beneath, often soon bordered or blotched with bronze purple colouring, white-felted and hairy beneath when young but mature leaves without felt. Leaf toothing coarse, mostly simple and somewhat uneven. Terminal leaflet elliptic or sometimes obovate, emarginate, shortly or longly acuminate, not normally abruptly pointed. *Panicle* usually cylindrical, often congested at the top and there forming a dense heavy cluster, below which it may be interrupted and leafy, the leaves 3-nate below and simple or bifid above, the simple ones often with long attenuate-cuspidate points recalling those of *R. cuspidiferus* L. & M., thinly strigose above and hairy and usually white-felted beneath. Rachis rather flexuose, 5-angled, with long strong declining prickles, dense patent hair and some felt, normally eglandular. *Sepals* triangular-ovate acuminate with rather abrupt fairly long hair-like point, hairy and felted, sometimes aciculate, reflexed in fruit, often red-based within. *Petals* somewhat crumpled, narrowly elliptical, pinkish or white, spreading horizontally and held well apart. *Stamens* white, much longer than styles.

Exsiccata: Herb. Rilstone no. 4904, Lambourne, July 1949 (typus); no. 337, Nanpean, August 1924; West Looe valley, July 1924, H. J. Riddelsdell, ref. no. 913.

One of the most abundant and widespread of Cornish brambles, and Mr W. C. Barton tells me that it was collected from the Plym valley, south Devon, by Rev. H. J. Riddelsdell. In Cornwall it has been given various names. Moyle Rogers agreed to the name *R. leucostachys* Sm. for a gathering from Trenance valley, Newquay (C. C. Vigurs, 3 July 1908), but this must have been intended in a very aggregate sense as it differs widely from *R. vestitus* Weihe & Nees in the moderately hairy stem almost lacking felt, the normally elliptic terminal leaflet, the different range of panicle form, and the elliptic petals almost twice as long as wide. *R. vestitus*, indeed, seems to be absent from Cornwall; I have seen no Cornish specimen. Other names under which, as shown by herbarium specimens, *R. Riddelsdelli* is recorded in Davey's *Flora of Cornwall* are *R. iricus* Rogers, *R. robustus* P. J. Muell., *R. pubescens* Weihe, *R. Godroni* Lec. & Lam., and *R. silvaticus* Weihe & Nees. The records in the *Flora* of *R. iricus* are something of a puzzle. *R. orbus* Watson (*R. iricus* var. *minor* Rog. & Ridd.) certainly occurs in quantity in east Cornwall but I have seen no form of *R. iricus* from west Cornwall. The clumps shown me by Tresidder at Polgoda, cited under *R. iricus* as 'Much the most characteristic British specimens that I have seen' (W. M. Rogers), are certainly *R. Riddelsdelli*, which varies considerably in appearance, being often a shaggy-looking plant in full exposure on the higher ground but soft and 'floury-looking' in some of the southern valleys. *R. Riddelsdelli* is probably better placed in the section Discolores of Rogers's *Handbook* than with his Vestiti.

6. **Rubus Thurstonii**, sp.nov. *Turio* obsolete angulatus, dense pilosus, aculeis reclinatis vel leviter curvatis ad angulos pro maxime parte dispositis, faciebus sulcatis vel planis vel convexis, glandulis stipitatis, aculeolis, aciculisque paucis instructus. *Folia* 5-nata, supra parce pilosa, subtus tomentosa, dense pilosa. Petioli sulcati. Foliolum terminale ellipticum vel obovatum, breviter acuminatum, integrum vel emarginatum. *Inflorescentia* pyramidalis vel oblonga, inferne foliosa. Rachis cum pedicellis dense tomentoso-pilosa, parce glandulosa vel eglandulosa, aculeis reclinatis falcatisve armata. *Sepala* tomentosa, pilosa, vulgo aculeata, post anthesin patula. *Petala* rosea. *Stamina* stylos superantia.

Stem rather low-arching, generally densely hairy, rather bluntly angled with flat or channelled faces. Prickles subequal, mostly on the angles, usually declining or somewhat curved; occasional pricklets or stalked glands on the faces. *Leaves* rather small and neat, mostly 5-nate, pedate or digitate; petioles and petiolules furrowed, very hairy and with falcate prickles. Leaflets with finely pointed nearly simple teeth, strigose above, thickly hairy and white or greyish felted beneath, the felt often becoming thinner later. Terminal leaflet generally obovate, occasionally elliptic, usually shortly acuminate or cuspidate-acuminate, veins sunken above and prominent on the lower surface. *Panicle* cylindrical or pyramidal with shortly-stalked primordial flower and strongly ascending to patent ascending or patent branches; leafy below with simple or 3-nate leaves, in form and clothing much like those of the stem, but terminal leaflets of the 3-nate leaves often strongly cuneate. Rachis, peduncles and pedicels with dense yellowish hair and felt, and with numerous curved or falcate prickles which are generally crowded on the pedicels. Stalked glands and acicles usually few or none. *Sepals* with dense yellowish hair and felt, often aciculate, patent in young fruit, sometimes loosely reflexed later. *Petals* pink. *Stamens* longer than styles.

Exsiccata: Herb. Rilstone no. 918*a*, Ventongimps, Perranzabuloe, 26 August 1935 (typus); 918*b*, Ventongimps, 26 August 1935; 38B, Restormel Road, Lostwithiel, 24 July 1920, Thurston & Rilstone; no. 193, near Callington, 13 August 1923, Thurston & Rilstone (more glandular form).

The plant is frequent over the Ventongimps area and the more glandular gatherings from Lostwithiel, Callington and elsewhere evidently belong to the same species. It seems allied to *R. pyramidalis* Kalt. and perhaps to *R. Schmidelyanus* Sudre. The eye is attracted to the clumps by the conspicuous patent sepals.

7. **Rubus carnkiefensis**, sp.nov. *Turio* purpureus, angulatus vel subteres, nitens. Aculei brevi recti vel reclinati, ad angulos dispositi. *Folia* ampla, 3–5-nata pedata, rugosa, supra strigosa, subtus plusminus tomentosa, pilosa, irregulariter subsimpliciter mucronato-serrata. Foliolum terminale convexum, late ovatum vel ellipticum, emarginatum, breviter acuminatum. *Inflorescentia* laxa, late pyramidalis, foliosa. Rachis flexuosa, piloso-tomentosa, aculeis plerumque falcatis armata. *Sepala* ovata, dense tomentosa, fructu patula. *Stamina* stylos superantia.

Stem purplish, fairly sharply angled or bluntly angled or roundish, almost glabrous, shining, prickles almost equal, patent or nearly so, short with slender points. *Leaves* 3–5-nate pedate, large, on stout petioles, recalling the leaves of *R. ramosus* Briggs, but somewhat rugose, strigose above, mostly green and hairy beneath or somewhat felted, toothing somewhat coarse and irregular but nearly simple, mucronate. Leaflets broad and overlapping, the basal leaflets on very short stalks. Terminal leaflet broadly ovate or elliptic, emarginate, shortly acuminate. *Panicle* lax, broad and leafy with large 3-nate to simple leaves, coarsely toothed and felted and hairy or green beneath; the ultra-axillary part broad and truncate with the primordial flower shortly stalked. Rachis stout and flexuose with dense yellowish hair and felt, and with long and slender falcate, declining or patent prickles. *Sepals* ovate with shortish attenuate points and close felt and hair, patent in fruit. *Stamens* longer than styles.

Exsiccata: Herb. Rilstone no. 1141, Mill Downs near Carnkief (typus); no. 2196, Ventongimps.

A frequent plant around Carnkief and Ventongimps and thence southward about seven miles to the Idless valley near Truro. In stem and leaf it looks rather like a coarse form of *R. ramosus* Briggs, but it is quite distinct from that species and is everywhere true to type.

8. **Rubus Newbouldianus**, sp.nov. *Turio* arcuato-prostratus, angulatus, leviter sulcatus, sat pilosus, aculeis subaequalibus rectis vel reclinatis plerumque ad angulos dispositis, setis et glandulis stipitatis inaequalibus brevibus instructus. *Folia* 5-nata, saepe luteo-viridia, saepe sat ampla. Foliola plicata, argute duplicato-serrata, supra leviter strigosa, subtus pilosa. Foliolum terminale sat anguste elliptico-obovatum, longe

acuminatum, breviter petiolulatum. *Inflorescentia* lata, truncato-pyramidalis, foliosa, dense pilosa, aculeis tenuibus rectis vel reclinatis, glandulis stipitatis inaequalibus multis brevibus vel brevissimis instructa. *Sepala* apice attenuata, in fructu reflexa. *Petala* anguste elliptica, rosea. *Stamina* alba stylos superantia.

Stem more or less prostrate, striate, angular with faces flat or concave, considerably hairy with simple and clustered hairs, usually with a fair number of acicles, short but unequal stalked glands, and an occasional pricklet. Stem prickles mostly confined to the angles, and of moderate length, a few longer or shorter, somewhat unevenly distributed along the stem, patent or slightly declining from a moderate base. *Leaves* of moderate size or rather large, sometimes in shade very large, 5-nate, usually pedate, generally yellowish green but sometimes darker green, strigose or glabrescent above, thinly hairy beneath and soft to the touch when young. Toothing rather deeply cut and finely pointed, usually simple in the lower part of the leaflets, more compound above with unequal variously directed teeth, sometimes more or less lobate. Leaflets plicate with the veins prominent underneath. Terminal leaflet broadest above the middle and gradually narrowed above to a moderate or rather long acuminate point, and usually somewhat narrowed below to the entire or slightly emarginate base; the shape varying usually from rhomboidal to somewhat narrowly elliptical, the outline generally rather narrow but sometimes rather broad and almost subrotund. *Panicle* broad with rather long peduncles, more or less pyramidal—the larger ones strikingly pyramidal—truncate above with the primordial flower short-stalked, often leafy throughout, lower branches erect-patent, many-flowered, upper branches erect-patent to patent, corymbose, often 5-flowered. In some panicles there is a considerable subracemos-corymbose ultra-axillary development. Rachis straight or slightly flexuous with numerous slender prickles mostly straight and slightly declining. Acicles usually few, occasionally gland-tipped; stalked glands numerous, unequal but short and rarely exceeding the rather dense shortish hair, some very short. Felt appears only on the peduncles, pedicels and sepals. *Sepals* rather broad, usually extending into a narrow appendage; externally clothed with grey felt, short hair, and numerous short-stalked glands, whitish felted within and often reddening at base, reflexed in fruit. *Petals* elliptical or ovate, clawed, not contiguous, deep pink at first, fading later. *Stamens* with long white filaments exceeding the green styles. Young carpels pilose.

Exsiccata: Herb. Rilstone no. 4905, Lambourne, July 1949 (typus); no. 651, Burras near Wendron, August 1929; no. 166, Polperro, October 1920.

Davey's *Flora of Cornwall* includes no record by name of '*Rubus Newbouldii*', but that of *R. radula* Weihe from near Connor Downs is shown by his specimens to belong to *R. Newbouldianus*. The species is, indeed, frequent throughout Cornwall and in Devon. It is what Rogers called 'Dartmoor *Newbouldii*'. Rev. H. H. Harvey has sent me a gathering from Bridestowe, north Devon. In Cornwall I have collected it from various stations from near Land's End to the valley of the Lynher. With its shortly-petioluled terminal leaflets, usually of narrow outline, and its broad pyramidal panicle, this is a very different plant from *R. rubristylus* Watson (*R. Newbouldii* of Rogers's *Handbook of British Rubi*).

9. **Rubus peninsulae**, sp.nov. *Turio* purpureus, obtusangulus, parce pilosus, ad angulos tomentosus, aculeolis paucis et glandulis stipitatis paucissimis instructus. Aculei parvi tenues inaequales, majores ad angulos dispositi. *Folia* 3–5-nata, plerumque 3-nata. Petiolus atropurpureus, parce pilosus, glandulis stipitatis et aculeis tenuibus falcatis vel reclinatis praeditus. Foliola subtus parce pilosa, supra strigosa. Foliolum terminale obovato-rhombeum, emarginatum, sat grosse mucronato-serratum. *Inflorescentia* plerumque pyramidalis, inferne foliosa, superne racemosa vel subracemosa. Rachis pilosa, aculeis tenuibus reclinatis sparsis et glandulis stipitatis inaequalibus confertis munita. *Sepala* fructu reflexa. *Petala* rosea, anguste obovata, patula. *Stamina* alba stylos superantia.

Stem dark purple, bluntly angled, slightly hairy and with lines of pubescence along the angles, at any rate in the early part of the season. Prickles small, unequal, mostly on the angles, declining, with a few pricklets and occasional stalked glands scattered on the faces. *Leaves* 3–5-nate pedate, but mostly 3-nate with petiolules of lateral leaflets at right angles to petioles. Leaflets strigose above, green and thinly hairy beneath when mature. Petiole dark purple, thinly hairy, usually with lines of pubescence, with some stalked glands and with the curved or declining prickles mostly rather weak. Terminal leaflet obovate-rhombic with cuneate emarginate base and abrupt shortish point. Leaf toothing rather coarse and shallow, mucronate, simple or somewhat compound with some teeth patent. *Panicle* usually pyramidal, leafy below with 3-nate and simple leaves, racemose or subracemose above with rather few slender declining acicular prickles, considerably to densely hairy with spreading white hair, little or much close felt in the upper part and with numerous unequal stalked glands and acicles, the larger glands exceeding the hair. Upper 1-flowered branches of panicle mostly patent. *Sepals* ovate-triangular with longish attenuate point, grey-felted, hairy and glandular, white-margined, reflexed in fruit. *Petals* pink, narrowly obovate, spreading. *Stamens* white with pink bases, exceeding the styles.

Exsiccata: Herb. Rilstone no. 36, Restormel, Lostwithiel, July 1920, Thurston & Rilstone; no. 262, New Bridge near Callington, 12 July 1924, F. Rilstone with H. J. Riddelsdell (typus); no. 685, near the Men-an-Tol, Penzance, July 1930; no. 460, between Luxulyan and St Blazey, 4 August 1926, F. Rilstone with E. Thurston; no. 2332, near Cargreen, Saltash, July 1939, W. B. Luke.

This Cornish plant, which I have previously recorded as *R. podophyllus* P. J. Muell. (det. H. J. Riddelsdell), occurs throughout the county from the Lynher valley to near Land's End but chiefly in the south-east, especially about Liskeard, Lostwithiel and Par. It is allied to *R. fuscicortex* Sudre, differing notably in the greater amount of hair and felt and the abundance of stalked glands on the panicle, the absence of felt under the stem leaves, the coarser leaf toothing and the usually bright pink petals. The specimens labelled '*R. podophyllus*' collected by F. H. Davey are not *R. peninsulae*. Some of them are *R. cinerosiformis* Rilst., which Mr W. Watson identifies with true *R. podophyllus* P. J. Muell., and which is certainly near that species but is, I believe, distinct from it. The only gathering of *R. peninsulae* which I have seen, apart from my own gatherings and W. B. Luke's from Cargreen, is one of F. H. Davey's from College near Penryn which is labelled '*Rubus rosaceus* (sp. collect.) subsp. *infecundus* Rogers, fide W. M. Rogers'.

10. **Rubus penhallowensis**, sp.nov. *Turio* angulatus, faciebus planis vel sulcatis, atropurpureus, fere glaber, aculeis longis tenuibus subaequalibus plerumque ad angulos dispositis, aculeolis et glandulis stipitatis multis vel paucis armatus. *Folia* sat ampla, atroviridia, plicata, et rugosa, supra fere glabra, subtus viridia. Foliolum terminale late ovatum cordatum, breviter petiolulatum. *Inflorescentia* laxe pyramidalis, foliosa. Rachis flexuosa, aculeis tenuibus inaequalibus, rectis vel reclinatis, glandulis stipitatis inaequalibus armata. *Sepala* fructu reflexa. *Petala* rosea non contigua. *Stamina* stylos valde superantia.

Stem moderately angled with flat faces or somewhat furrowed, deep purple in exposure, with little or no hair. Main prickles long and slender, mostly on the angles, not very uneven in size. Smaller armature of pricklets, often gland-tipped, and stalked glands of various lengths often very unevenly distributed on the stems, some stems or parts of a stem very sparsely provided, others abundantly. Mature *leaves* rather large, dark green, plicate and rugose, almost glabrous above, paler green beneath and hairy on the veins. Petiole with hooked prickles and stalked glands, slightly hairy. Leaf toothing rather coarse and shallow, mucronate. Terminal leaflet broadly ovate-cordate, short-stalked. *Panicle* laxly pyramidal, leafy to within a short distance of the top, with lower leaves 3-nate and uppermost lanceolate; all coarsely toothed. Rachis somewhat flexuous, dark purple where exposed to light, with slender declining or patent prickles of varied length and unequal stalked glands, the latter crowded on the pedicels and upper part of the rachis, very thinly hairy, with white patent hair, on lower part of rachis, considerably hairy in upper part, not felted. *Sepals* reflexed in fruit, ovate-triangular passing abruptly into a short hair-like point, whitish-margined, hairy, felted and glandular. *Petals* of moderate size, smoothly concave, well separated. *Stamens* pinkish, much longer than green styles.

Exsiccata: Herb. Rilstone no. 4906, Lambourne, July 1949 (typus); no. 386, Callestick, August 1925.

Fairly frequent over an area of several square miles around Penhallow and Callestick, Perranzabuloe. Previously recorded by me as a form of *R. sagittarius* Ridd., det. H. J. Riddelsdell. It differs from that species in its broad, convex, non-felted leaflets, the non-felted hairy rachis, the sepals reflexed on the fall of the petal, etc.

11. **Rubus coombensis**, sp.nov. *Turio* arcuato-prostratus, angulatus, pilosus, aculeis parvis, sat inaequalibus, reclinatis, aculeolis et glandulis stipitatis sat numerosis armatus. *Folia* plerumque 3-nata. Foliola supra strigosa, subtus laxe pilosa, viridia. Foliolum terminale oblongum, acuminatum, cordatum, mediocriter serratum. Inflorescentia inferne foliosa, laxe subracemosa vel cylindrata vel laxe late pyramidalis, dense pilosa, aculeis rectis vel reclinatis et glandulis stipitatis numerosis instructa. *Foliola inflorescentiae* subtus viridia. *Sepala* fructu patula vel subpatula. *Petala* anguste elliptica. *Stamina* stylos superantia.

Stem low-arching, distinctly angled, striate when dry, very considerably hairy especially on the angles (often quite shaggy on the angles but sparingly hairy on the faces). Principal prickles rather small, unequal, declining, chiefly on the angles; on the faces a fair number of minute stout pricklets and fairly many mostly short but unequal stalked glands, a few long. Stem colour dull brownish purple. *Leaves* 3–4-nate, mostly 3-nate, not large. Petiole hairy with a few stalked glands sunk in the hair, some stoutish falcate prickles and a few declining weak ones. Leaflets thinly hairy beneath, strigose above. Terminal leaflet distinctly oblong, $2\frac{1}{2}$–4 times as long as its stalk, acuminate with narrow cuspidate point and cordate base. Teeth shallow, rather coarse but finely pointed. *Panicle* rather small or of moderate size, laxly racemose or cylindrical to broadly shortly pyramidal, leafy below with leaflets green and hairy, not felted, beneath. Rachis and its slender branches with slender patent or declining prickles, dense spreading hair and felt, and numerous unequal stalked glands mostly sunk in the hair. *Sepals* with close dark grey felt and some spreading hair and a few acicles and stalked glands, white-margined, subpatent in fruit. *Petals* spreading, long and narrow. *Stamens* exceeding styles.

Exsiccata: Herb. Rilstone no. 418, near Coombe Junction, Liskeard, 10 July 1926; no. 552, Coombe near Liskeard, 28 August 1927, Thurston & Rilstone (typus).

A frequent plant over an area of some square miles south and west of Liskeard and also in Herb. G. T. H. Fleming from the Devonshire side of the Tamar at Greystone Bridge. It has been recorded as a form of *R. curvidens* A. Ley. Otherwise it seems to have been overlooked. It differs from *R. curvidens* in its low growth, smaller mostly 3-nate leaves, smaller simpler panicle with panicle leaves green, not grey-felted, beneath, its patent or subpatent sepals and its small narrow petals.

12. **Rubus Vigursii**, sp.nov. *Turio* ex arcu humile procumbens, supra ruber, subtus viridis, subglaber, acutangulus, faciebus planis, aculeis aculeolisque inaequalissimis hinc illinc dispositis, reclinatis vel rectis, interdum falcatis, aciculis et glandulis stipitatis rubris paucis vel multis instructus. *Folia* parva, 3–5-nata pedata. Petiolus longus pilosus aculeis falcatis glandulis stipitatis rubris munitus. Foliola supra strigosa subtus pilosa viridia, plerumque simpliciter et inaequaliter dentata. Foliolum terminale obovatum cordatum sensim acuminatum. *Inflorescentia* parva cylindrica superne truncato-racemosa, inferne foliosa laxa. Rachis tomentosa, aculeis aciculis et glandulis stipitatis multis inaequalissimis rubris instructa. *Sepala* tomentosa, glandulosa, aciculata, sat longe acuminata, patula. *Petala* angusta alba. *Stamina* alba stylos superantia.

Plant small and low-growing; *stem* low-arching or prostrate, bright crimson above, green beneath, almost without hair, sharply angled with flat faces. Prickles and pricklets abundant, mostly straight with slender sharp points, patent or slightly declining, very unequal, scattered, a few falcate. Stalked glands and acicles few or many. *Leaves* small 3–5-nate, pedate on long petioles with numerous unequal curved prickles, stalked glands and some hair. Leaflets strigose above, hairy beneath, with rather shallow mostly simple but rather irregular toothing, most teeth crimson-tipped and some patent. Terminal leaflet obovate cordate with point gradually acuminate to almost triangular. Basal leaflets very shortly stalked. *Panicle* small cylindrical, racemose and truncate above with primordial flower often sessile and the one-flowered branches patent, lax and leafy below, the leaves mostly 3-nate with terminal leaflets often rhombic. Rachis and its branches generally with little hair but with some felt and numerous very unequal slender prickles, acicles and stalked glands, all as a rule bright red and the longest glands much exceeding the diameter of the pedicels. *Sepals* felted, abundantly glandular and aciculate, of varied length but usually moderately long-pointed, acuminate, patent in fruit except in the primordial flower where they are sometimes loosely reflexed. *Petals* narrow, white. *Stamens* white, much longer than the styles.

Exsiccata: Herb. Rilstone no. 4, Polperro, east Cornwall, July 1919 (typus); no. 28, Polperro, July 1920; no. 268, below Cadsonbury Camp near Callington, 12 July 1924.

Of frequent occurrence in most of the valleys on the south side of the watershed as in those of the Lynher, Seaton, Looe, Polperro and Fal and in one locality, Ventongimps, north of the backbone of the county. It is the Cornish representative of *R. Koehleri* Weihe & Nees.

The Structure and Development of Eriocaulon septangulare With. By Dr C. Leighton Hare

(With Plate 22 and 40 Text-figures)

(Communicated by Prof. J. McLean Thompson, M.A., D.Sc., F.L.S.)

[Read 7 June 1945]

Introduction

Eriocaulon septangulare With., the subject of the present study, is a small, submerged aquatic plant, the sole European representative of a large genus of well over two hundred species, the great majority of which are plants of swampy soils, with a wide distribution in the tropical and subtropical regions of both hemispheres. The present species occupies an extensive tract in the north-eastern United States and the adjacent parts of southern Canada, but elsewhere is found only along the western seaboard of Ireland and in a few isolated localities in the Hebrides. Thus it belongs to the small group of less than a dozen plants, of diverse affinities, that together constitute the North-American element in the British flora. The whole region within which *E. septangulare* is found in our islands forms but a very small outlier, separated from the main area of the species in North America by two thousand miles of open ocean. This striking discontinuity in the geographical range of the plant, its occurrence far to the north of the bulk of the genus, its presence on both sides of the Atlantic but its absence from the mainland of Europe, together with its restricted distribution within the British Isles—collectively these facts present a complex of problems of peculiar interest.

A good deal of discussion has centred around the North-American species in our flora, and the problems involved have given rise to much speculation and not a little controversy, but progress in solving them may well have been hindered by the tendency to regard the group as a homogeneous one. The questions at issue are admittedly difficult, and, if a further advance is to be made, a fresh approach seems necessary. A full list of the plants comprising the North-American element, together with a summary of their distribution, will be given in a later paper and it need only be stated here that they differ from one another not only in their natural affinities and their life forms, but also in their means of dispersal, their habitat requirements, and their respective ranges. Nor can we assume that the manner of their introduction to Britain and the time of their arrival here are necessarily the same for each of them. It would, in fact, be true to say that every member of the group really presents a distinct and separate set of problems. The most promising approach would therefore seem to be to confine attention to a single species. The present study is concerned solely with *E. septangulare*. Its primary aim has been to examine afresh the questions raised by its peculiar geographical distribution and to shed some further light on these, but more especially to arrive at a clearer understanding of the restricted range of the species within the British Isles.

From the outset it became clear that little progress could be looked for until the biological equipment and autecology of the species had first of all been investigated; for these, together with certain historical factors, must have determined its present distribution. With this end in view, field studies have been carried on over a number of years, at first in Ireland, and later in the Hebrides. At the same time the plant has been grown in culture under various conditions on a considerable scale, while further information has been gleaned from transplant experiments carried out at several localities in Scotland. In this way the life history of the plant has been worked out and a general picture of its climatic and edaphic preferences and tolerances gradually built up, though many details of this picture still remain to be filled in.

Special attention has also been devoted to the structure and development of the species, for although the relationship between structure and function may not always be entirely clear, there can be no doubt that the morphology and anatomy of a plant will often illuminate its particular mode of life and the nature of its adjustment to its environment. This is perhaps especially true when, as in the present instance, the species is a fully submerged aquatic while the genus as a whole is predominantly terrestrial.

For convenience, the results obtained in the course of the investigation will be described in two papers. The first of these, presented here, deals with the morphology and anatomy of *E. septangulare* and their relation to its environment. The second paper, to follow later, will give an account of its biology and ecology, and will include a full discussion in which the geographical distribution of the species will be re-examined in the light of the facts which have emerged as the work proceeded.

PREVIOUS LITERATURE RELATING TO *ERIOCAULON*

Apart from taxonomic studies, which do not concern us here, the literature relating to the genus *Eriocaulon* is not extensive, while the present species has hitherto received but little attention.

In 1888 Poulsen published a paper on the anatomy of the family Eriocaulaceae. He selected a series of types, representing each of the genera included at that time in the family, and one species of *Eriocaulon* (*E. helicrysoides*) was described. In 1903 there appeared W. Ruhland's comprehensive monograph on the family Eriocaulaceae. In this work, the detailed systematic descriptions are preceded by an introductory chapter giving a general account of the range of structure met with in the family, and there are some isolated references to the present species. A paper by Holm (1904) dealt with some features of interest in the histology of a single American species of *Eriocaulon* (*E. decangulare*): further reference will be made to this paper in describing the anatomy of *E. septangulare*.

The French systematist Lecomte, in addition to describing a number of Chinese, Indo-Chinese, and Madagascan species of *Eriocaulon*, published three papers in 1908 dealing with some points of interest in the biology and anatomy of some of them. In one of these he gives an account of the remarkable method of dispersal of the fruits and seeds of two species from swampy ground in Indo-China. In these, the sepals have undergone a peculiar modification to form a float, closely resembling in shape the shell of a nautilus, whereby the fruits are prevented from sinking and are wafted on the surface of the water to emergent land, where germination can take place under conditions favourable to the establishment of the seedling. In another paper Lecomte discusses the nature of the curious glands, found near the tips of the petals in species of *Eriocaulon*, and provides some evidence for his belief that these structures are really nectaries. In his third contribution Lecomte shows how certain anatomical peculiarities of the scape can be employed as an aid to the identification of some species of *Eriocaulon*.

In 1919 another French botanist, L. A. Malmanche, published a thesis dealing with the comparative anatomy of the Eriocaulaceae and some adjacent families, mainly with a view to establishing their real affinities. A short general review of the anatomy of the Eriocaulaceae is given in Part IV of Solereder and Meyer's *Systematische Anatomie der Monocotyledonen* (1929), in the course of which there are occasional references to *E. septangulare*. In a comparative treatment of the structure of monocotyledonous seedlings, Boyd (1932) described the mature seedling of a single unidentified species of *Eriocaulon*. Her interpretation of this seedling, which differs from that of the present writer, will be fully discussed in a forthcoming communication.

Finally, there are three papers dealing specifically with *E. septangulare*. A lucid account of its embryology and floral development (referred to again later) was given by Smith in

1910. A brief paper by Solomon (1931), on some features of the anatomy of the rhizome and root, displayed some confusion of thought and was marred by inadequate and misleading illustrations. Adam, in 1933, described the successful cultivation of *E. septangulare* at the Royal Botanic Gardens, Edinburgh, but recorded the failure of all attempts to obtain germination of its seeds.

No comprehensive account of either the anatomy, ecology, or geographical distribution of *E. septangulare* has hitherto appeared.

(*a*) Morphology

General habit of growth

E. septangulare is, in its normal state, a fully submerged aquatic species, growing rooted in the substratum beneath still waters. It is a gregarious plant, and in favourable habitats will often cover considerable areas with a close, continuous sward. Plate **22**, fig. 1 shows a small colony of flowering individuals, left stranded above water during a period of drought; but the general habit of growth is best displayed by an isolated specimen and will be gathered from Plate **22**, fig. 2, which shows a plant in vegetative condition after two seasons' active growth in culture.

Although the structure of the flowers is usually very constant, in other respects the species is a variable one, individuals differing much in size and vigour, as well as in the dimensions and proportions of the several organs. The more extreme forms encountered in the field will be dealt with later, and the following description is based on typical average individuals growing under normal conditions.

The plant has a short, tapering rhizome up to 5 cm. long and 5 mm. at its widest part attached to the substratum by very numerous adventitious roots, and terminating in a rosette of bright green, narrow, sharply pointed leaves. The rhizome is creeping and, i allowed sufficient room, grows forward horizontally over the soil surface, but in closely packed colonies may assume an oblique or almost vertical position. As growth proceeds throughout the warmer months new leaves continuously unfold, while the older ones progressively die away, so that once maturity is reached the terminal leaf rosette remains practically constant in size, while the greater part of the rhizome is then devoid of leaves Each season a fresh increment of some 2–4 cm. is added to the rhizome, while the portion formed in the previous season shrivels up as its food reserves are depleted, leaving only the vascular cylinder (which often persists as a tough, hard core for one or more years longer). The appearance of the plant towards the end of the season, with its Iris-like horizontal rhizome, terminal leaf rosette and abundant roots, can be clearly seen in Pl. **22**, fig. 2, which shows also on the right the shrunken remnants of the previou season's growth. During the winter months the plant enters on a period of rest and active growth ceases, although the leaves of the rosette remain green and are not shed.

Ramification of the rhizome and vegetative reproduction

Branching of the rhizome can take place in two quite distinct ways: (i) by sympodia branching, which is always associated with flowering; and (ii) by monopodial branching which is of rarer occurrence, and usually found in sterile individuals only.

(i) *Sympodial branching*

The inflorescence is invariably terminal in position and the growing point is used u in its formation. At the onset of flowering in early summer two buds arise in the axil of the uppermost leaves immediately surrounding the base of the young scape, one bu on each side. As the scape elongates these buds develop into axillary branches, bot growing at the same rate, so that by the end of the season two fresh increments of rhizom have been formed, diverging at an angle of about 20°. This sympodial method of branchin is illustrated in Text-figs. 1–3, where the plants have been sketched after removal of a he leaves except those of the axillary shoots, while in Text-fig. 2 the scape also has een cut off so as to display more clearly the forking of the rhizome. Text-fig. 1 shows he condition at the beginning, Text-figs. 2 and 3 that at the end of the summer. As a rule, xillary branches do not produce inflorescences in the season in which they are formed, ut in specially vigorous individuals they sometimes do so. When this happens, ramifiation of the rhizome is carried a stage further, for rudimentary branches of the second rder are always laid down at the base of the secondary inflorescences, and in conequence, the rhizome may fork twice or thrice in a single season. This condition is llustrated in Text-fig. 4, where *I* is the main inflorescence, and s_1 and s_2 the new axillary hoots at its base (all other leaves having been removed). It will be seen that s_1 terminates ı a young secondary inflorescence *i*, while s_2 has remained sterile.

ii) *Monopodial branching*

Not all specimens of *Eriocaulon* flower in a given season, and those which do not, requently remain unbranched, but sometimes they resort to monopodial branching; uds arising in the axils of leaves some way from the growing point of the rhizome. Ionopodial branching of flowering specimens is a rare occurrence, but it has been noted on ne or two occasions: it seems to be associated with arrested development of the terminal nflorescence. In Text-fig. 5, which illustrates this condition, *a* and *b* are the normal ympodial branches at the base of the inflorescence *I*, while *c* and *d* are additional axillary ranches of approximately the same age, arising from the upper surface of the rhizome.

Branching of the rhizome of *Eriocaulon*, whether sympodial or monopodial, endows he species with an effective means of vegetative increase; for as the older parts of the hizome progressively decay, the branches become isolated, each of them henceforth eading an independent life. Once established in a suitable habitat, the plant can in onsequence spread rapidly.

The root and root-system

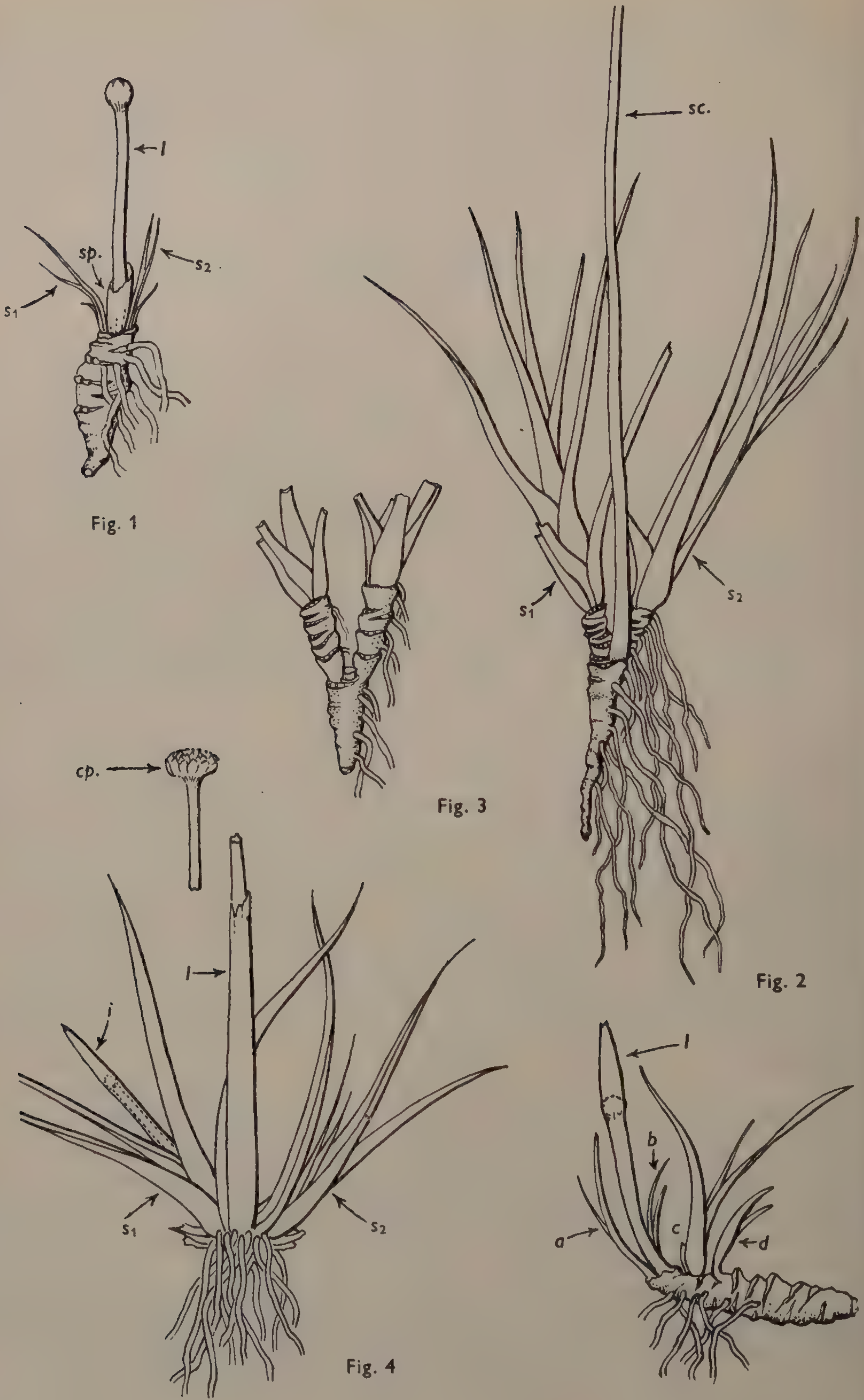
On fertile soils *E. septangulare* produces a vigorous and well-developed root system see Pl. **22**, fig. 2); on sterile or sandy substrata it is much reduced. The individual roots re all adventitious and arise mainly from the lower surface of the rhizome, often breaking hrough the bases of the leaves. They are pure white and translucent, soft in texture, very exible and have a curious and characteristic vermiform appearance, owing to the resence of regularly spaced internal diaphragms. In well-grown specimens they have n average diameter of about 1 mm. and taper but little, except near the extreme tip. he great majority do not branch at all, but occasionally the more vigorous ones produce few very slender, secondary or tertiary branches. Root-hairs are entirely lacking. In ontrast to the leaves, all the roots formed during the growing season persist until the ollowing spring.

The leaf

The leaf arrangement is two-ranked in the seedling but changes gradually to a rather omplex spiral as the plant matures. The phyllotaxy is then difficult to determine exactly, ecause the horizontal or oblique position of the rhizome in relation to the incident light esults in a displacement of the leaves. The individual leaves, which are linear-lanceolate ı shape with a concave upper surface, are broadest just above the base and then taper radually to a very fine point. Their maximum length is about 7 cm. and their width bout 5 mm., but they are often smaller than this. Soft and rather brittle in texture and right green in colour, they are markedly translucent, and show a characteristic internal enestration, due to certain anatomical peculiarities which are described later.

The spathe and scape

The onset of the reproductive phase in the early summer is marked by the emergence the spathe in the centre of the leaf rosette; it takes the form of a narrow cylindrical heath, open only at the extreme tip (Text-figs. 4, 5). Growing at first more rapidly than



Text-figs. 1–5. For legends see p. 427.

e scape, it forms a protective sheath within which the inflorescence slowly develops, it after reaching a length of some 3–5 cm. it ceases to elongate, and shortly afterwards e young capitulum breaks through the tip. This sequence of events is illustrated in . **22**, figs. 3–5, which show how effectively the young inflorescence is protected through it the early stages of its development within the spathe. The latter serves also as an cessory organ of assimilation; in colour, texture and internal structure it resembles leaf in all respects except for its cylindrical form.

The scapes of *E. septangulare* are very variable in length, but in this respect show close correlation with the depth of water in which the plant is growing. In very shallow ater they may not exceed a few inches, while in deeply submerged specimens they ach several feet. In North America they are stated to reach 3 m. (Moldenke, 1937), hile Praeger (1934) reports scapes up to 3 ft. long in Ireland, but in Skye the writer nds that they rarely exceed 2 ft. In proportion to their length they are remarkably arrow, with a diameter (in an average specimen) of about 3 mm. just above the base, nd tapering gradually to about half of this at the apex. These dimensions are, moreover, dependent of the length of the scape, which is so buoyant that it needs but little echanical support. The cross-section is polygonal with projecting angles, but in spite the specific name of the plant, the number of angles is by no means always seven. or example, out of ten scapes, all of approximately the same length, four showed six, ur others seven, while one had eight, and one nine sides. As it develops, the inflorescence axis frequently becomes spirally twisted.

The inflorescence

The inflorescence is a capitulum closely recalling that of some Compositae and Dipcaceae and in the present species is almost spherical when young, though it becomes roadly elipsoidal and vertically flattened as it matures (compare Text-figs. 1, 4). t the same time the colour changes from nearly black to pale grey as the flowers unfold. he involucral bracts are usually five, though sometimes six in number, and the receptacle strongly convex and rounded on its upper surface. The flowers, each of which is subnded by a bract, are arranged in successive concentric whorls, which develop in centritetal order; the members of any one whorl open simultaneously, although those near the ntre of the capitulum seldom reach maturity.

The total number of flowers in a given capitulum bears little relation to its size, although large heads of about 8 mm. in diameter the average number approximates one hundred. he flowers are always unisexual, but the distribution of the two sexes within the capiulum is very variable and shows a number of features of interest. Although often escribed as monoecious, this condition is in fact far from universal, unisexual heads also ccur, and these may be either male or female; again in monoecious heads although the owers of any one whorl are always of one sex, the distribution of sexes within the heads ows great variability. Flowers of different sexes do not occur in alternate whorls nor e they always grouped together near the centre or at the periphery of a head, as stated some Floras; the arrangement is, in fact, irregular and unpredictable and varies from ead to head. These and other features relating to the capitula are illustrated in Table 1,

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ext-figs. 1–5. General morphology of the plant and mode of branching of the rhizome. Text-fig. 1. A plant at the beginning of the growing season, showing the young axillary shoots s_1 and s_2 at the base of the developing inflorescence *I*. *sp*., base of spathe (the rest has been removed). (× 1.) Text-fig. 2. A plant at the end of the growing season, showing the fully developed axillary shoots s_1 and s_2 diverging from the base of the scape *sc*. (× 1.) Text-fig. 3. Base of same plant as in Text-fig. 2, after removal of scape, showing sympodial branching of the rhizome. (× 2.) Text-fig. 4. Plant in which one axillary shoot s_1 has produced a secondary inflorescence *i*. *cp*., capitulum; *I*, base of inflorescence. (× 1.) Text-fig. 5. Plant showing sympodial branches *a* and *b* at the base of the inflorescence *I*, and additional branches *c* and *d* arising farther back along the rhizome. The young capitulum is still enclosed in the spathe. (× 1.) [*Note*. In all the plants figured above, leaves (other than those of the branches) have been removed.]

which shows the results of flower counts in a series of capitula of different kinds ar sizes. It will be seen that in five of the capitula, all of about 8 mm. diameter, the tot number of flowers ranged from 96 to 137, while in two others, both about 6 mm. diameter, the numbers were 30 and 72 respectively. Again, in the monoecious heads t ratio of female to male flowers varied from less than 1 to over 14, though, on the averag female flowers considerably exceed the male in any one capitulum. It should be add that among the unisexual heads the female greatly predominate; only one entirely ma head has in fact been noted among the large number examined (see no. 7 in Table It is clear that in *E. septangulare* there is an effective mechanism for securing cros pollination, for in monoecious individuals the sexes are separated in time of developmer while in dioecious ones there is spatial segregation. In a mixed colony, however, mar flowers of both sexes will mature simultaneously.

Table 1

No.	Diameter of capitulum (mm.)	Total no. of flowers	Male flowers	Female flowers
1	About 8	97	36	61
2	,, 8	96	52	44
3[1]	,, 8	137	9	128
4	,, 6	72	30	42
5	,, 8	100	0	100
6	,, 8	122	0	122
7	,, 6	30	30	0
		Total 654	157	497

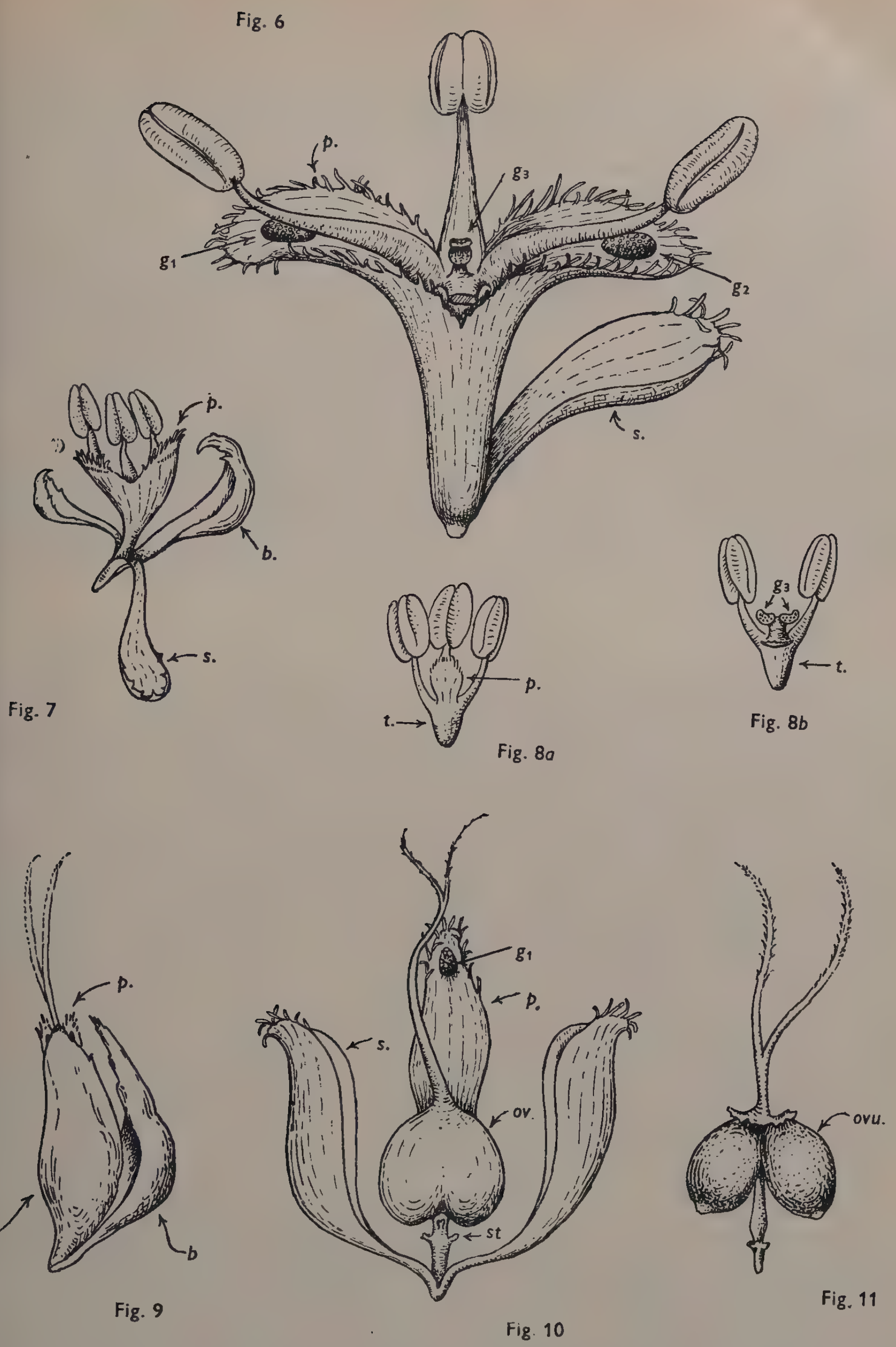
[1] In capitulum no. 3 in the table the nine male flowers were confined to the outermost whorl.

The flowers

The morphology of the flower of *Eriocaulon* presents certain difficulties, and contr dictory statements are still to be found in the literature regarding it. This uncertain can be attributed in part to the minute size of the flowers, which do not exceed 2 mm. length, and partly to the fact that in the course of development, the form and arrang ment of the parts become much modified by intercalary growth. Hence, it is only following its ontogeny that the morphology of the flower can be interpreted with co fidence. The structure of both male and female flowers is, on the whole, uniform ar constant, but a considerable number have been found which depart in various wa from the normal type: these will be described in a separate paper, and the account whi follows refers to normal flowers only. It should, however, be mentioned that the exceptional flowers provide evidence for the belief that the unisexual and dimerous flowe of *E. septangulare* have been derived by reduction from an ancestral type which h perfect ones constructed on a completely trimerous plan.

(i) *The female flower*

This is shown in bud, just before opening in Text-fig. 9 and fully developed in Tex fig. 10 (after removal of the bract and the anterior petal, so as to display the gynaeciu to better advantage). The two sepals, strongly concave and bearing a terminal tuft glistening white hairs, completely enclose the flower when in bud, but partially separa and become reflexed at the tip during anthesis. The two petals are free and strap-shape tipped with white hairs and provided on the upper surface with an ovoid, subtermin glandular structure, whose real nature and function have long been in doubt. Usua referred to in taxonomic descriptions simply as a gland, Lecompte, in 1908, suggest that it might be a nectary and (working apparently with herbarium material) he obtain



Text-figs. 6–11. Morphology of the flower. Text-fig. 6. Fully developed male flower, after anthesis. (× 20.) Text-fig. 7. Immature male flower with subtending bract. (× 20.) Text-fig. 8*a*. Very young male flower, after removal of sepals. (× 25.) Text-fig. 8*b*. The same flower, after removal of petals and two of the stamens. (× 25.) Text-fig. 9. Nearly mature female flower, before anthesis. (× 20.) Text-fig. 10. Fully developed female flower, after anthesis; one petal removed. (× 20.) Text-fig. 11. Gynaecium of female flower, with ovary wall dissected away. (× 20.) [*b*., bract; *s*., sepals; *p*., petals; g_1 and g_2, petal glands; g_3, gynaecial glands; *st*., staminodes; *ov*., ovary; *ovu*., ovule.]

some evidence that in two Indo-Chinese species of *Eriocaulon* these petal glands secret a reducing sugar. In the present species it was found possible to collect and test th actual secretion from the glands of living flowers and the results of these tests, couple with observations on the behaviour of visiting insects (to be described later), make i clear that at least in *E. septangulare* these petal glands do in fact function as nectaries The bilobed, bilocular ovary is shortly stipitate, and terminates in a style of variabl length with two divergent, hairy stigmas. Each loculus contains a single orthotropou ovule, pendulous from its upper and inner extremity. Occasionally, one of the ovule fails to develop, but as a rule each gives rise to an ellipsoidal or subspherical seed, which when mature, completely fills its loculus. In Text-fig. 11 a mature gynaecium is shown with the ovary wall dissected away so as to reveal the ovules and their mode of attachment to better advantage. Immediately beneath the heart-shaped ovary and attached t the short stalk which supports it are four minute emergences, arranged in two pairs lyin respectively in the anterior-posterior and lateral planes, one pair inserted slightly abov the other (see Text-fig. 10). Though extremely small, these structures are alway present in the living flower, yet they have been generally overlooked, and in taxonomi descriptions are very rarely referred to. They were noted, however, by Saunders (1939 who (presumably on comparative grounds) regarded them as staminodes. Some of th abnormal flowers found by the present writer provide conclusive evidence that thi assumption is correct.

(ii) *The male flower*

This is also dimerous in arrangement, as seen in Text-fig. 7, which is a sketch of young male flower, together with its subtending bract. Text-fig. 6 shows, on the same scale, a male flower just as it reaches maturity, but before dehiscence of the anther (the bract and one sepal have been removed). The two sepals are free, but the corolla gives at first the impression of having a trumpet-shaped tube with two divergent lobes and this is how it has usually been interpreted. Thus Hooker (1930) describes the inne perianth of *Eriocaulon* as 'a two- to three-lobed tube' and speaks of the stamens a 'inserted on the tube'. A very similar statement is made by Le Maout & Decaisne (1873) while more recently Rendle (1930) says 'the petals form in the male a two- to three-lobed tube, on the upper part of which stand the stamens'. In contrast to these authors Ruhland (1903) and Hutchinson (1934) describe the petals as 'free' but do not refer t the mode of insertion of the stamens. It is evident, therefore, that the morphology of th male flower presents some difficulty and that it has been interpreted in different ways b different workers. The difficulty arises because of the extensive intercalary growth of th axis in the development of the flower of *Eriocaulon* (a fact first emphasized by Smith i 1910). This makes it necessary to study the early phases of development if the structur of the mature flower is to be rightly understood.

Text-figs. 8*a*, *b* show a very young male flower: in (*a*) the sepals have been removed and in (*b*) the petals and two of the stamens in addition. At this stage it is easy to remov the petals, leaving all four stamens *in situ*, when it becomes clear (1) that the latter ar inserted directly on the floral axis, and (2) that the part of the flower below the level o insertion of the stamens is solid, not hollow. Evidently, therefore, this portion of th flower should be regarded as a torus, on the rim of which both petals and stamens ar inserted; during the later stages of development the torus grows rapidly, and eventuall simulates a corolla tube very closely; but the appearance is deceptive and careful examination at sufficient magnification reveals its true nature.

Each of the petals is provided on its upper surface with a subterminal gland, large than those of the female flower, while the nectar-secreting mechanism of the male flowe is further augmented by two additional glands at its centre. The latter are U-shaped an occupy the upper surface of a shortly stalked organ, which terminates the floral axis an rises slightly above the level of insertion of the stamens (Text-fig. 6). This organ is forme at an early stage in the development of the flower, just as the stamens are, and in the very young flower represented in Text-fig. 8*b* it can be clearly seen. There can be little doubt that it should be regarded as gynoecial in origin; hence it provides additional evidence of the derivation of the unisexual flower of *Eriocaulon* from an ancestral type having perfect flowers.

The seed

The seed, which is ellipsoidal in shape, is about 0·8 mm. long by 0·5 mm. wide and has a light brown, smooth, tough and elastic testa (Text-figs. 12, 14). It is almost filled with the white, starchy endosperm, while the minute undifferentiated embryo (whose greatest dimension scarcely exceeds 0·2 mm.) is situated at the extreme micropylar end. In taxonomic works, the embryo is usually referred to as 'lenticular', though Smith (1910) is more precise and speaks of it as 'bell-shaped, with flaring edges'; neither description, however, quite conveys its true shape. When isolated from the seed and carefully examined it is seen to have the form of a bi-convex lens, with a hemispherical process at the centre of one of its faces. It lies within the seed with this process immediately opposite to and directed towards the micropyle, so that when viewed from either end of the seed, the embryo appears circular, while in longitudinal sections it has the shape shown on the right of Text-fig. 13.

Embryology

A full account of the early stages in embryology is given in the paper by Smith (1910), already referred to, and here it need only be said that he found that the development is unusual, the embryo at first passing through regular quadrant and octant stages, while a suspensor is entirely absent. His account ends by emphasizing the striking lack of differentiation of the resting embryo as it is found within the mature seed; 'at this stage', he says, 'there is no differentiation of the embryonic organs, nor any indication where these shall have their origin'. This statement forms a fitting starting-point for the description given below of the post-seminal maturation of the embryo and the development of the seedling proper. The account should be regarded as a preliminary one, for it is based on external morphological features only, and for this reason is couched in somewhat general terms. A fuller and more critical account and a comparison with other monocotyledonous seedlings are in course of preparation and will be presented as soon as the histology of the embryo and seedling has been fully worked out.

Germination

On account of the lack of differentiation of the resting embryo the germination of *E. septangulare* necessarily takes place in two stages, though the transition between them is a gradual one. The first stage covers the maturation of the embryo outside the seed and the second the development of the seedling proper until it becomes established as a self-nourishing plantlet.

Stage 1. *The maturation of the embryo*

The seed tends to settle on the substratum beneath the water with its long axis horizontal or nearly so, as shown in Text-figs. 12 and 14. In this position the lenticular portion *p.* of the resting embryo (Text-fig. 13, right) lies in the vertical plane, with the process on its outer face immediately opposite the micropyle. When germination begins in late spring or early summer the embryo first enlarges slightly, the inner face becoming nearly hemispherical. The process (*p.*, Text-fig. 13) then elongates and soon breaks through the micropyle, appearing as a short, colourless, cylindrical body with a rounded end, which grows forward horizontally till it reaches a length of about 1 mm. (Text-fig. 12). If at this stage the complete embryo is dissected out of the seed, it is seen to be mushroom-shaped, as shown on the left of Text-fig. 13 (its parts are lettered to correspond with those of the resting embryo, so that the relation between the two will be apparent).

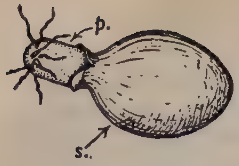


Fig. 12

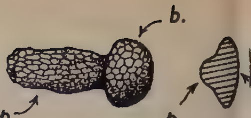


Fig. 13

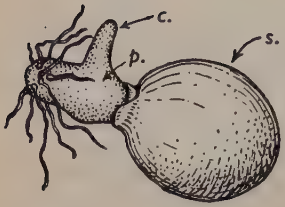


Fig. 14

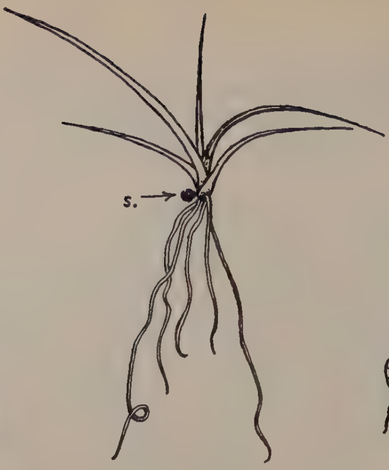


Fig. 20

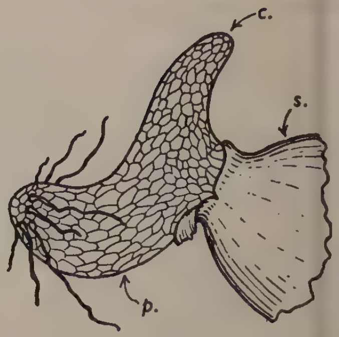


Fig. 15

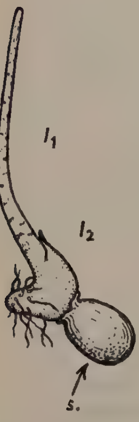


Fig. 16

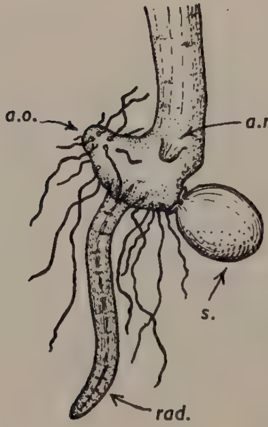


Fig. 17

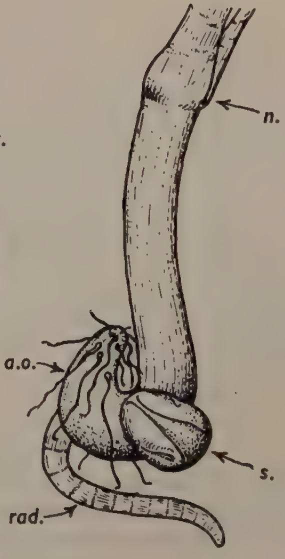


Fig. 18

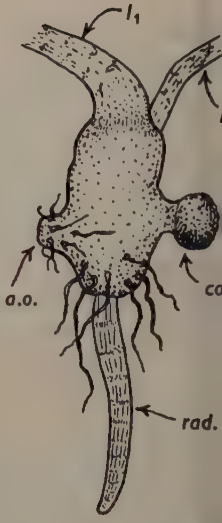


Fig. 19

Text-figs. 12–20. Morphology of the seed, embryo and seedling. Text-fig. 12. First stage in germination, the embryo emerging from the micropyle. (×16.) Text-fig. 13. On the right the restin embryo in longitudinal section; on the left the young embryo dissected from the seed. (Bot ×26.) Text-fig. 14. Second stage in germination. (×16.) Text-fig. 15. Another embryo a same stage as Text-fig. 14, to show lack of differentiation. (×32.) Text-fig. 16. Third stage i germination showing the first leaf and rudiment of the second. (×12.) Text-fig. 17. Fourt stage in germination, emergence of the radicle followed by the first adventitious root. (×12 Text-fig. 18. Another seedling at the same stage as Text-fig. 17, but showing the epicotyl, th first node, and the strongly curved anchoring organ. (×12.) Text-fig. 19. A further seedlin of the same age, but possessing a definite hypocotyl. The seed has been dissected away to revea the 'cotyledonary sucker'. (×12.) Text-fig. 20. A seedling 3 months old, showing the matur habit, the seed still attached at the base, and one of the coiled roots. (⅔ natural size.) [*n.*, firs node; l_1, first leaf; l_2, second leaf; *rad.*, radicle; *a.o.*, anchoring organ; *cot.*, cotyledon; *s.*, seed For other reference letters see text.]

The distal end of *p.* now becomes clothed with a crown of rather stiff hairs, many of which are backwardly directed, and a few days later a conical process *c.* arises on the upper side of *p.* and half way along it. This grows vertically upwards until its length is about equal to that of the horizontal portion from which it arises, so that the embryo as a whole is now shaped like an inverted letter T (see Text-figs. 14, 15). Up to this stage, the embryo is still colourless and undifferentiated, but the apex of *c.* now turns green and a growing-point is organized here which gives rise to the plumule. With this event the first stage in germination may be considered to end, for it is immediately followed by the appearance of the first rudimentary leaf.

Stage 2. *The development of the seedling*

The embryo at this time is still extremely small (its greatest dimension hardly yet exceeds 1 mm.), but the first leaf grows rapidly and, after it has reached a length of a few millimetres, the rudiments of a second one can just be discerned. The young seedling now presents the curious appearance shown in Text-fig. 16 and it will be seen that there is as yet no sign of a radicle. The latter organ, which in most plants is the first to emerge on germination, is in the present species the last to appear. About this time, however, it breaks through the base of the seedling at a point vertically beneath the plumule: it appears to be endogenous in origin. The axis of the seedling proper is now defined and it will be seen that it is approximately at right angles to the embryonic axis (Text-fig. 17). The hairs, at first confined to the tip of the axis, meanwhile gradually increase, and when the radicle has reached a length of a few millimetres, they usually cover the whole under surface of the seedling.

The hemispherical structure embedded in the seed is clearly the absorbing tip of the greatly reduced cotyledon (the so-called 'cotyledonary sucker') which is united to the body of the seedling by a very short cylindrical limb passing through the micropyle. This is made clear in Text-fig. 19 which shows a seedling at a slightly later stage, where the seed coat has been torn open and removed so as to reveal the structure within. That part of the seedling which lies below the level of insertion of the cotyledon is usually very much abbreviated, so that a hypocotyl can hardly be said to exist. Often, however, there is a slight downward extension of the axis here, and occasionally a short but quite definite hypocotyl is laid down (compare Text-figs. 17, 19). The epicotyl is better developed, but it rarely exceeds a few millimetres in length; occasionally, however, it grows somewhat larger, so that at this stage the seedling may have quite a slender appearance, as in the example sketched in Text-fig. 18. Subsequent internodes are always very short so that the seedling soon assumes the squat appearance and rosette habit of the mature individual (Text-fig. 20). The first adventitious roots arise in the epicotyledonary internode (Text-fig. 17), the later ones in successively higher internodes, but the time of their appearance varies considerably in different individuals.

Throughout the whole period of germination the seed remains firmly attached in a lateral position at the base of the epicotyl, where it is held in place by the pressure of the testa around the cylindrical limb of the cotyledon, which is always of smaller diameter than the absorbent tip embedded in the seed (Text-fig. 19). The seed is, in fact, held in this way so effectively that it continues in position long after germination is complete. It can be seen, for example, at the base of the leaf rosette in Text-fig. 20, which is a sketch of a seedling known to be 4 months old, since it had been grown from seed.

Anchorage of the seedling

As noted above, the radicle is the last of the organs to appear, and long before it does so the seedling has become lighter than water, for even the first leaves are provided with the abundant aerenchyma which is so characteristic of every part of the mature plant. In the absence of a radicle, some alternative mechanism must therefore be present for securing the young seedling to the substratum, otherwise it would inevitably rise to the surface and all hope of its establishment would then vanish. In the initial stages c germination, anchorage is effected by the distal end of the embryonic axis with its crow of hairs. This may remain horizontal or, more frequently, bend more or less strongl upwards (compare Text-figs. 16–18); it becomes entangled in the particles of the sub stratum, holding the seedling in place, until fixation is later on secured in the normal wa by the roots. The mechanism recalls a grappling hook and does, in fact, function in th same way. In the mature seedling this curious anchoring organ appears as a lateral out growth at the base of the epicotyl, on a level with and opposite to the cotyledon (Text fig. 19), but as explained above, it is actually a product of the still undifferentiate embryo and is the first part to emerge from the micropyle when germination begins Clearly this specialized anchoring mechanism is needed most urgently throughout th first phase of germination (i.e. while the embryo is undergoing maturation outside th seed) and also during the second phase, up to the time when the radicle and later th adventitious roots appear. Towards the end of this period anchorage is rendered mor secure by the growth of hairs from the lower surface of the maturing embryo: the specia mechanism, however, remains functional until germination is well advanced. The nee for secure anchorage of the seedling even at a relatively late stage is emphasized by th frequent occurrence of twisted or coiled roots. An example of the latter condition i shown in Text-fig. 20, where one of the roots has coiled through 360° (presumably aroun some object embedded in the substratum). Coiling of the roots, though uncommon, ha been reported in several other aquatic species (see Arber, 1920, pp. 205–6).

(*b*) ANATOMY

The leaf

When examined in surface view the leaf reveals beneath its epidermis, even to th unaided eye, a regular and highly characteristic reticulation, and under a magnificatio of 15 diameters a short segment of it presents the appearance shown in Text-fig. 22. Th structures responsible for this elaborate pattern are made clear by transverse sections such as that shown diagrammatically in Text-fig. 24 which was taken across the lowe third of the leaf. The sinuous outline, most pronounced on the abaxial face, is due to th presence of a series of longitudinal ridges alternating with shallow furrows, which exten from the base to the apex of the leaf. Internally, the leaf is traversed longitudinally b a series of air canals (*a.c.*), each of which lies opposite one of the ridges and is crossed a regular intervals by a succession of transverse diaphragms, dividing the space withi into compartments about 0·5 mm. long. The canals are separated from one another b strips of parenchymatous tissue through the centre of each of which runs a single vascula bundle (*v.b.*); hence the bundles are situated opposite to the surface furrows. It is thes internal structures, seen through the translucent epidermis of the leaf, which produce th characteristic reticulation referred to above. Owing to the gradual narrowing of the lea the number of air canals seen in any transverse section steadily decreases as the sectio approaches the apex. For example, a well-grown leaf about 3 in. long showed thirtee canals at its base; 2 in. higher they were reduced to six in number, while at the apex onl the central one remained. There is a corresponding reduction in the number of vascula bundles, each of which pursues an independent course and remains unbranched in it passage through the leaf.

The structure and disposition of the assimilatory tissue show marked specializatio There is first a single hypodermal layer of chlorenchyma (shown cross-hatched in Tex fig. 24), whose component cells have their long axes parallel to the leaf surface. This tissu is shown in surface view in Text-fig. 25, and it will be seen that it forms a loose meshwor with abundant intercellular spaces. The assimilatory tissue of the leaf is further augmente by the diaphragms, whose thin plate-like cells are richly provided with chloroplasts, givin them a vivid green colour, in striking contrast with the adjacent colourless parenchym

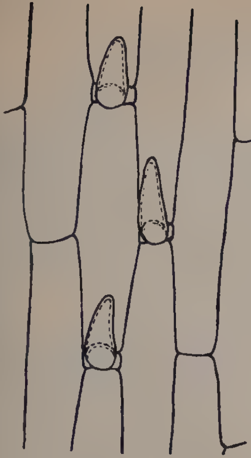


Fig. 21

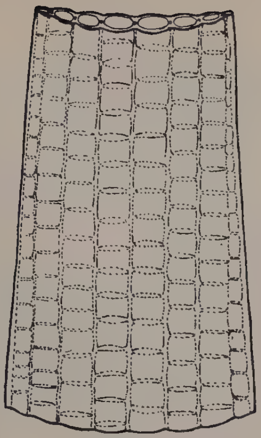


Fig. 22

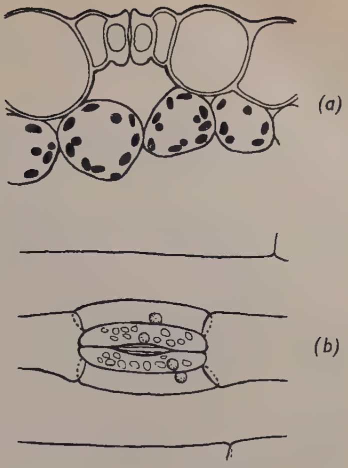


Fig. 23

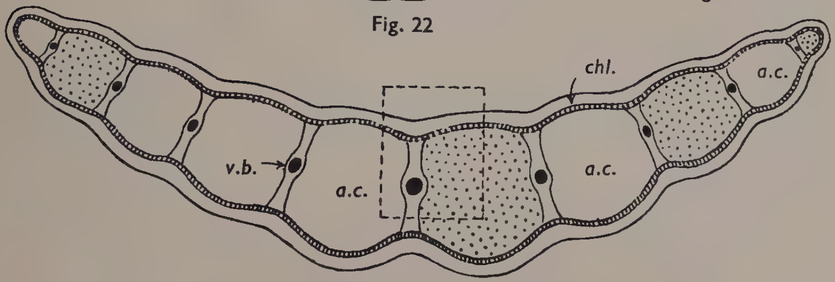


Fig. 24

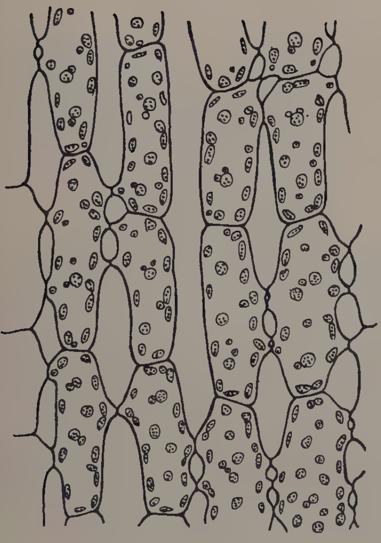


Fig. 25

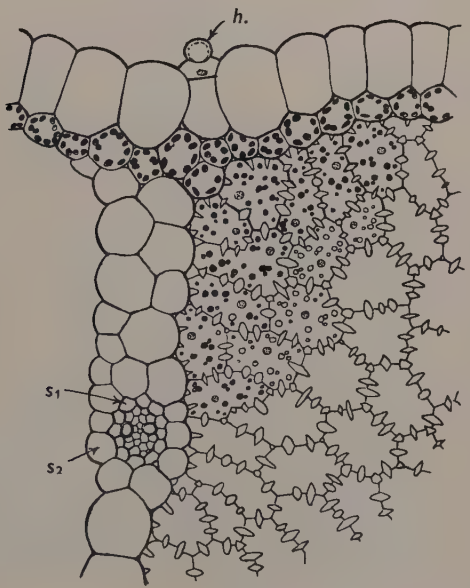


Fig. 26

Text-figs. 21–26. Anatomy of the leaf. Text-fig. 21. A portion of the epidermis, showing the small conical hairs. (×150.) Text-fig. 22. A segment of the leaf under low magnification, showing the characteristic fenestration. (×15.) Text-fig. 23*a*, *b*. A stoma in section and surface view. (×340.) Text-fig. 24. A diagrammatic transverse section of the leaf. (×20.) *a.c.*, air canal; *v.b.*, vascular bundle; *chl.*, subepidermal chlorenchyma; diaphragms shown dotted. Text-fig. 25. The subepidermal chlorenchyma in surface view. (×350.) Text-fig. 26. Shows under high magnification the area enclosed by broken lines in Text-fig. 24. (×160.) s_1 and s_2, the inner and outer sheaths of the vascular bundle; *h.*, hair in transverse section. The chloroplasts, which are shown in black, are omitted on the right of the diaphragm.

The area enclosed by dotted lines in Text-fig. 24 is drawn under high magnification in Text-fig. 26. It shows the large radially elongated epidermal cells, the single layered hypodermal chlorenchyma, a portion of one of the partition walls which separate the air canals, with its central vascular bundle, and finally to the right a part of one of the diaphragms. The cells of the latter exhibit the elaborate stellate outline and numerous small intercellular spaces so characteristic of these structures in hydrophytic species (the abundant chloroplasts are shown in black).

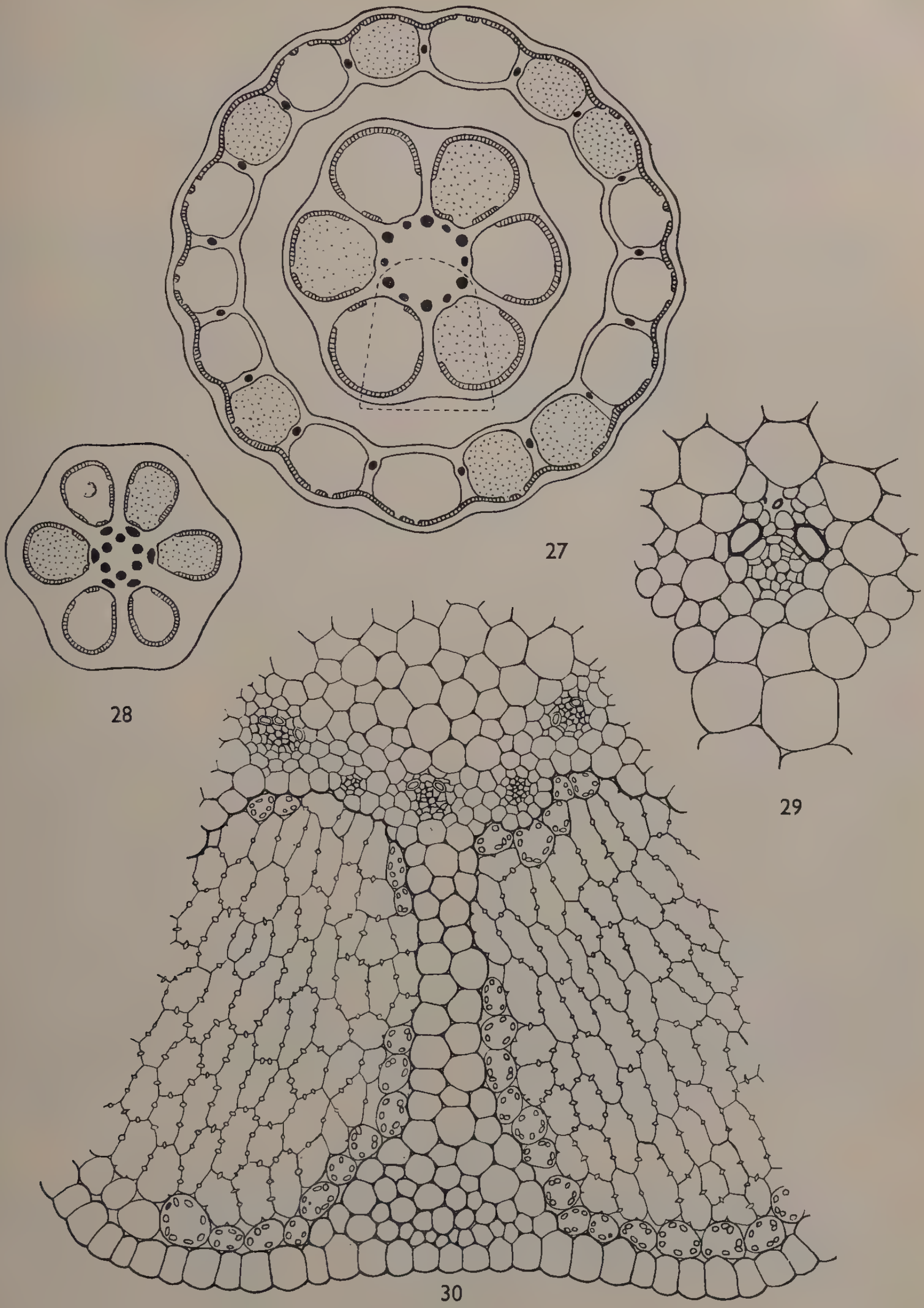
The vascular tissue of the leaf is a good deal reduced, though less so than in many submerged aquatic plants. Each of the larger bundles has several vessels, always spirally thickened, but otherwise thin-walled and scarcely lignified: in the smaller bundles there may be only a single vessel. The phloem is poorly differentiated and consists mainly of parenchyma. Surrounding each bundle is a well-marked sheath of small cells, yellowish in colour, with slightly thickened walls and elongated in the direction of the veins. Considerable discussion has centred around the so-called double bundle sheaths of the leaves of Eriocaulaceae. Poulsen (1888) described them as occurring in the leaves of all the genera he studied, including *Eriocaulon*, and they were referred to also by Ruhland (1903) and Boyd (1932). Holm (1904), in his study of *E. decangulare*, concluded that the outer sheath had little real validity, since its cell structure was indistinguishable from that of the adjacent collenchyma of the mesophyll: moreover, the sheaths were lacking in other parts of the plant. In *E. septangulare* there is also an apparent double sheath surrounding the vascular bundles of the leaf only, but the outer layer is ill-defined, and examination shows that it is composed of cells which differ only in size from those of the parenchymatous tissue within which the bundle is embedded (Text-fig. 26).

The epidermal cells of the upper and lower faces of the leaf are similar; narrowly rectangular in shape, they have smooth, thin, non-sinuous walls and contain no chloroplasts. Although the leaves appear at first sight to be quite glabrous, examination shows that both surfaces bear regular longitudinal rows of small, bluntly pointed hairs; the latter are arranged in narrow parallel bands, lying within the furrows of the leaf, but absent, or nearly so, from the ridges. A small portion of the epidermis bearing three of the hairs is shown in surface view in Text-fig. 21, while one of them is seen in vertical section in Text-fig. 26. Each of the hairs comprises a small rectangular basal cell (cut off from the underlying epidermal cell) and a conical terminal cell, bent over so as to lie parallel to the leaf surface, with its tip directed towards the leaf apex.

Although in ordinary circumstances the leaves of the present species are continuously submerged, they are, nevertheless, provided with stomata of quite normal appearance. The latter are, however, confined to the abaxial surface and are present only in very small numbers, with a frequency of the order of 10 per cm.^{2}. One of them is shown in surface view and in section in Text-fig. 23*a*, *b*. The guard cells are in the plane of the epidermis; they are thickened in the usual manner and each is in contact with a subsidiary cell of about the same size lying parallel to it. A further feature of the leaf, unexpected in a submerged aquatic species, is the presence of a hydathode at its distal end. Near the apex the converging veins (here reduced to about three in number) unite to form a single large one which extends almost to the extreme tip where there is a single terminal aperture through which contact is made with the surrounding water. The significance of the presence of stomata and hydathodes on the submerged leaves of *E. septangulare* is considered in the final discussion.

The spathe

In discussing the morphology of the spathe its resemblance to a leaf was emphasized, and this impression is reinforced when it is studied anatomically. Internally the two organs are indeed almost identical, as will be apparent when Text-fig. 27, (a diagrammatic transverse section of the spathe surrounding the scape), is compared with Text-fig. 24, a corresponding section of the leaf. The air canals, diaphragms, and vascular tissue are closely similar in both organs, and the same is true of their surface features and the



Text-figs. 27–30. Anatomy of the spathe and scape. Text-fig. 27. Diagrammatic transverse section of the base of the scape and the surrounding spathe. (The tissues are shaded to correspond to those of the leaf.) (× 26.) Text-fig. 28. Diagrammatic transverse section of apex of scape. (× 26.) Text-fig. 29. One of the large vascular bundles of the scape. (× 490.) Text-fig. 30. Shows under high magnification the area enclosed by broken lines in Text-fig. 27 (× 114) (chloroplasts omitted from cells of the diaphragm).

distribution of the stomata. In the spathe, however, assimilatory tissue is not found beneath the inner epidermis, and the parallel vascular bundles show occasional anastomoses, especially as they approach the tip; but these minor differences only emphasize the essential similarity in structure of the two organs, which should clearly be regarded as homologous. It is of interest to note that in *E. decangulare* studied by Holm (1904), the anatomical resemblance between the leaf and spathe is also very close.

The scape

The main anatomical features of the scape are illustrated diagrammatically in Text-fig. 27 (the centre portion), and Text-fig. 28, which show transverse sections across its middle and upper regions respectively, the different tissues being shaded in a similar manner to those of the leaf and spathe. It will be seen that the scape exhibits striking radial symmetry, its wide cortex being traversed by a series of very large air canals, one opposite each of the superficial ridges. The canals are crossed at frequent intervals by diaphragms closely resembling those of the leaves. Separating the canals are radial plates of colourless parenchyma, expanded at their outer ends, which are feebly collenchymatous. The vascular system is simple and consists of a single ring of bundles surrounding the central medullary region; a large bundle opposite each of the ribs and a small one opposite each canal. Each of these conducting strands pursues an independent course, but on approaching the top of the scape the smaller ones bend inwards, so that a transverse section in this region shows the bundles in two concentric circles, as seen in Text-fig. 28. Just beneath the capitulum anastomoses take place between both series, and a complex vascular plate is established, from which small branch traces pass out horizontally to the involucral bracts and vertically to each of the flowers.

The area enclosed within dotted lines in Text-fig. 27 is shown on an enlarged scale in Text-fig. 30. It includes a portion of two of the diaphragms which, like those of the leaf and spathe, are single layered, exhibit very numerous intercellular spaces and are provided with abundant chloroplasts (to avoid confusion these are omitted in the figure). The canals are, in addition, lined with assimilatory tissue in the form of a loose reticulum, one-cell thick, whose meshes become wider on the inner, poorly illuminated wall of the canal. One of the large vascular bundles is illustrated in detail in Text-fig. 29. Here there are two vessels only, though sometimes a few smaller ones are also present; but the protoxylem is almost always broken down by the rapid elongation of the scape. The vascular bundles of the scape are without sheaths, nor is there any structural indication of an endodermis. It is noteworthy that there are no peripheral bundles in the scape, whose vascular system is in fact unusual for a monocotyledonous plant, since, except at the extreme summit, it comprises only a single ring of bundles occupying a central position, as seen in Text-fig. 27.

Table 2

Scape no.	Stomatal frequency per mm.^{2}	
	At base	At apex
1	9·20	16·50
2	7·26	8·33
3	7·96	14·70
	Total 24·42	39·53
	Average 8·14	13·18

In surface features there is again a close parallel with the leaf; lines of hairs occupying the furrows, while stomata are found in longitudinal rows overlying the intervening ridges. The stomatal frequency is of considerable interest, for whereas on the leaf it is of the order of about 10 per cm.^{2} on the scape it has an average value of approximately 10·7 per mm.^{2}, i.e. over one hundred times as great. A number of counts were made in order to determine if the frequency was constant or not throughout the length of the scape, and the results are embodied in Table 2.

The figures are in each instance the average of twenty separate counts, made from strips of epidermis removed from the lower third and upper third of the scapes respectively. The final average figures are thus based on sixty separate counts and show that the frequency at the top of the scape is over 60% greater than at its base; a result whose significance is dealt with later when the structure of the plant in relation to its environment comes under review.

The rhizome

Text-fig. 31 is a diagrammatic transverse section across the middle region of the rhizome, drawn to the same scale as that of the scape, while Text-fig. 33 shows on a large scale a small portion of the inner cortex and the vascular cylinder. The latter is very narrow, with a diameter less than a quarter of that of the whole rhizome, and comprises an outer ring of small almost contiguous bundles, enclosing a group of larger ones, scattered irregularly, the whole series inter-connected by numerous anastomoses (Text-fig. 33). In each bundle phloem predominates, the xylem being considerably reduced, with the vessels feebly lignified and only spirally thickened. The stele is bounded externally by a narrow band of sclerenchyma but possesses no true endodermis. The parenchymatous cells of the stelar region contain abundant starch which is not found elsewhere in the plant save in the endosperm of the seeds. The very wide cortex, traversed radially by numerous leaf traces, and in its lower half by the large adventitious roots, shows two distinct tissue zones (see Text-fig. 31); a narrow outer one of compact parenchyma beneath the radially elongated epidermis, and a wide inner one composed of narrow, thin-walled, cylindrical cells, longitudinally elongated and provided with numerous, radially arranged, spine-like processes by which alone the cells make contact with one another (shown in detail in Text-fig. 32). Thus the whole of this zone is permeated by innumerable, narrow, interstitial spaces, providing the rhizome with a continuous internal atmosphere; a further example of the elaborate provision for aeration which is so characteristic of the species.

In the apical portion of the rhizome, where the imbricated leaf bases protect the internodal surface, the latter is clothed with fine, white, silky hairs. These are multicellular and uniseriate, tapering gradually to a very fine point: though variable in length, they may reach 5 or 6 mm. The longer ones are remarkable for the extreme tenuity of the narrow, cylindrical cells of which they are composed, for these may reach a length of 1400μ, although their average diameter is but 20μ, i.e. the cells may be as much as seventy times as long as they are broad. On the older parts of the rhizome devoid of leaves the hairs break away, leaving the surface almost glabrous.

The root

In certain respects the root of *E. septangulare* is the most highly specialized of all its organs. There is very elaborate provision for the effective aeration of all its parts, its most striking feature being the occurrence of numerous, evenly spaced, cortical diaphragms; structures which, as already noted, give the roots the curious vermiform appearance so characteristic of the species. While diaphragms are present in various forms in many other parts of the plant, in the root they attain a degree of complexity unapproached elsewhere. Moreover, in the root they exhibit a striking radial symmetry, and the relationship of their component cells both to one another and to the intervening cortical cells is remarkably precise and regular. In the description which follows, it should be understood that the root is assumed to be in a vertical position and hence with all its transverse planes horizontal.

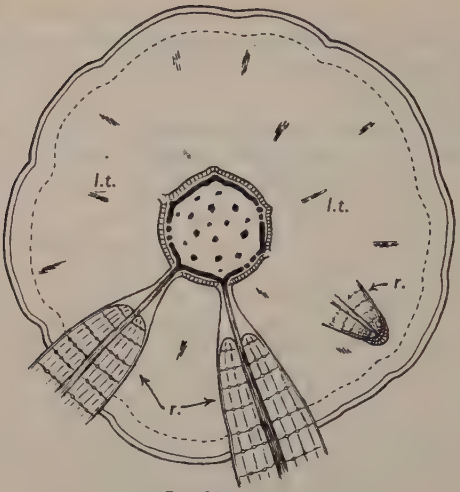


Fig. 31

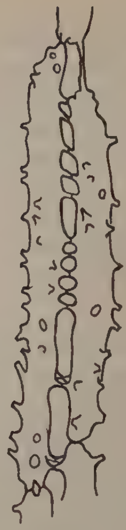


Fig. 32

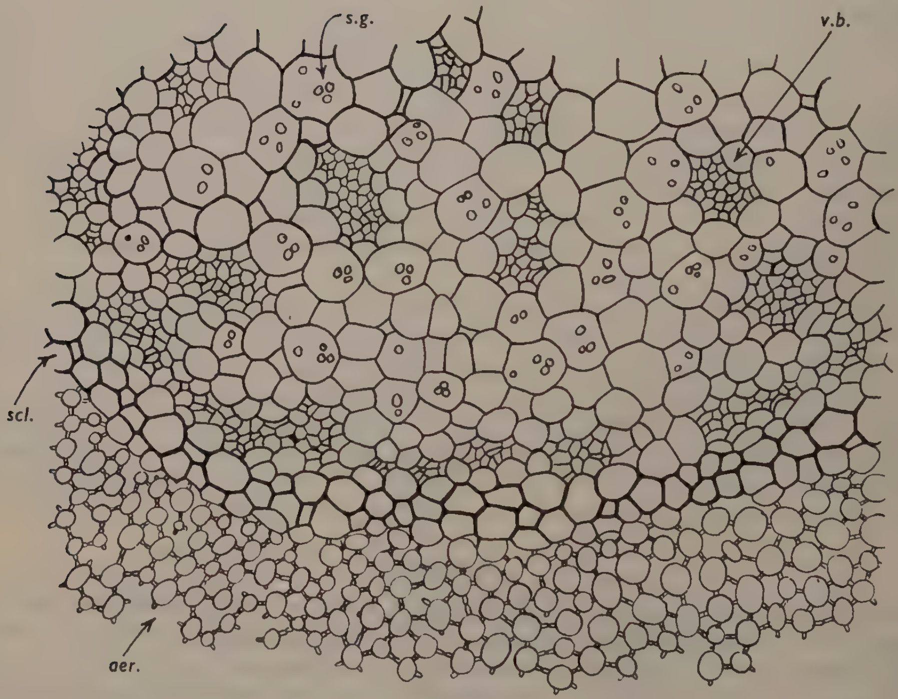


Fig. 33

Text-figs. 31–33. Anatomy of the rhizome. Text-fig. 31. Diagrammatic transverse section across the rhizome showing the central stele, the many small leaf traces *l.t.*, the adventitious roots *r*. The dotted line marks the boundary between the two zones of the cortex. (× 19.) Text-fig. 32. Two cells from the inner zone of the cortex drawn at high magnification, showing the spinous processes by which they make contact. (× 290.) Text-fig. 33. Small portion of the stele and adjacent inner cortex. (× 290.) [*s.g.*, starch grains; *v.b.*, vascular bundles; *scl.*, sclerenchyma; *aer.*, aerenchyma of cortex.]

There is a normal growing point and root cap, but root-hairs are entirely lacking. Immediately behind the apical meristem the cortex is homogeneous, but at a distance of approximately 1 mm. from it the diaphragms begin to appear. At first they are crowded closely together, so that in the second millimetre of length about ten occur, but the interval between them rapidly increases and soon attains its maximum and nearly constant value of approximately 0·5 mm. Longitudinal and transverse sections of the root tip and of the mature parts of the root not only display successive stages in the ontogeny of its stelar and cortical tissues, but also show how the regular spacing of the diaphragms is brought about. The cortical cells are at first all alike; they are thin-walled, isodiametric and arranged symmetrically in very regular radial files. Later, as growth and differentiation proceed, alternate transverse layers of cells behave in a different way. The cells of one such layer elongate rapidly in the direction of the axis of the root, but apart from a slight increase in diameter remain unchanged, so that when mature they give rise to a short cylinder of elongated, thin-walled parenchyma about 0·5 mm. long. The cells of the next layer do not elongate, but undergo elaborate change of shape and slight thickening, to form one of the thin, rigid, disk-like diaphragms described in detail below. This sequence of events is repeated with perfect regularity in all succeeding layers, so that in longitudinal section the cortex of the root shows a regular alternation of long and short cells, as seen in diagrammatic form in Text-fig. 34. The portion of this figure enclosed within dotted lines is drawn to a larger scale in Text-fig. 35. The stele (*s.*) is surrounded by a cylindrical sheath of two layers (sh_1) and (sh_2), whose component cells exhibit in less extreme form the structure already noted in the cortical cells of the rhizome (cf. Text-fig. 32): the sheath is in consequence permeated by intercellular spaces. In the radial longitudinal plane of Text-fig. 35 the cells of the diaphragm *d.* have a relatively simple outline, for their horizontal faces are smooth and lie in contact with the rounded ends of the long parenchymatous cells above and below them, but as seen in transverse sections of the root they have an extremely complex shape. This will be apparent from Text-fig. 38, which shows two of them in accurate outline drawn from a projected image. In the right centre of the figure they are seen in plan, above and below at (*a*) and (*b*) are sections along the planes *AA* and *BB* respectively, while to the left at (*c*) is a section along *CC*, the radial longitudinal plane of the root. The central part of these cells is approximately cylindrical, but each has a thin marginal flange in the transverse plane broken up into a highly complex series of narrow, almost linear lobes, which appear to be due to radial and tangential strains, accompanied by local lesions of the middle lamella. Each of the cells has four main lobes, projecting diagonally one from each corner; and if these alone are retained and all minor lobing is omitted, the cell outline can be reduced to the simplified diagrammatic form shown at (*d*) in Text-fig. 38.

Text-fig. 39 shows a sector of a complete diaphragm. Although semi-diagrammatic, it is drawn to scale, with the cells in their true relative positions, but in order to avoid confusion these have been given the simplified outline just referred to: in this way the structure of the diaphragm as a whole can be more clearly displayed. The stele in the centre (shown shaded) is surrounded first by two rings of sheath cells and then by five concentric rings of diaphragm cells. It will be seen that, in the inner rings, strictly radial alinement of the cells is maintained, and adjustment to the increasing circumference of successive rings is effected merely by a steady increase in the size of their component cells. When the latter become unduly large (this happens first in ring 3 in the figure) one or more of them in each ring is attached in the next outer ring to two smaller ones. In the figure this is seen in each of the cells lettered *a* to *e*, the outer ends of which have in each instance bifurcated, so as to provide the surfaces of contact for the two smaller cells joined to them in the following ring. The effect of this adjustment is that in the outer rings the number of cells per ring steadily increases, so that the strict radial symmetry of the diaphragm breaks down. It will be clear, however, that besides preserving a highly characteristic shape the cells are linked together throughout the diaphragm in

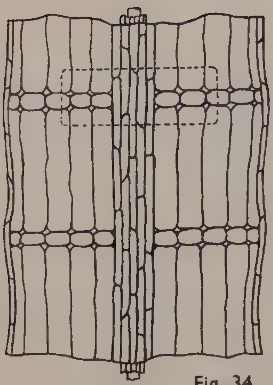


Fig. 34

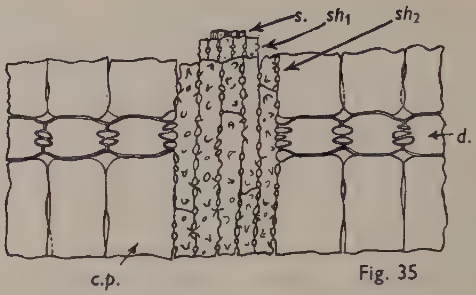


Fig. 35

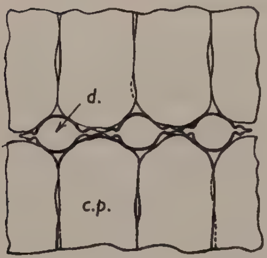


Fig. 36

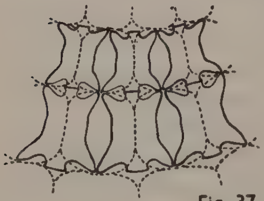


Fig. 37

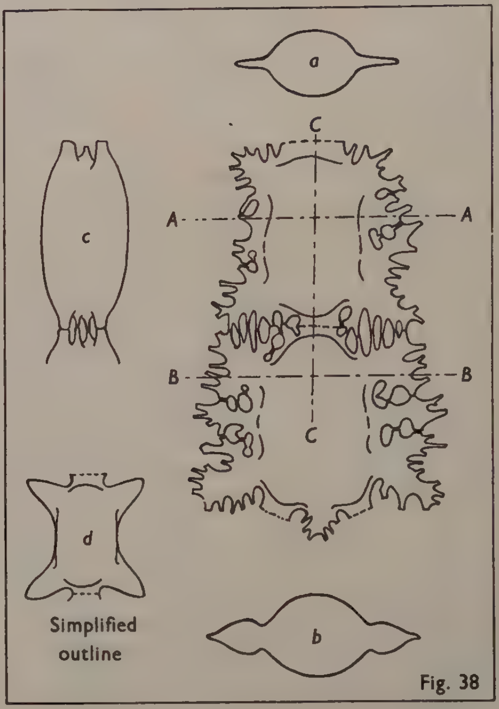


Fig. 38

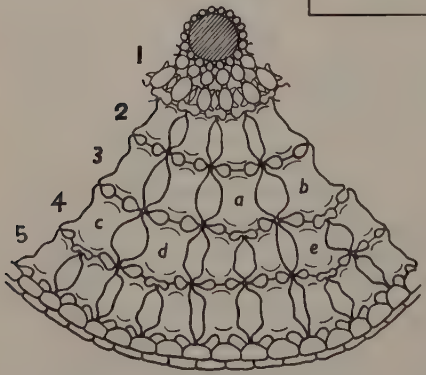


Fig. 39

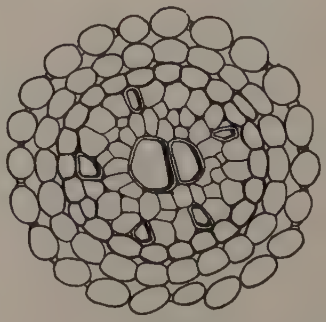


Fig. 40

Figs. 34–40. For legends see p. 443.

a remarkably precise and regular manner. This is further emphasized by the constant spatial relationship between the diaphragm cells and those of the cylinders of parenchyma immediately above and below them; as indicated in Text-fig. 37, where a few cells of a diaphragm are drawn with the overlying parenchymatous cells (shown by dotted lines) superimposed upon them. If this figure is compared with those showing the radial and tangential sections of the root (Text-figs. 35, 36) it will be clear that while each complete ring of diaphragm cells corresponds in position with a ring of parenchymatous cells immediately above it, the individual cells of the two systems regularly alternate.

Text-figure 40 is a transverse section of the central part of a root and shows the stelar tissues in detail. The endodermis has its cell walls uniformly but only slightly thickened. The phloem is a good deal reduced, but the xylem is fairly well-developed and usually takes the form of a single, large, central vessel (though two are not infrequent) surrounded by a varying number (three to five) of smaller ones, which almost always abut directly on to the endodermis, so that the pericycle is interrupted at these points. Long ago van Tieghem (1891) drew attention to this peculiarity in the roots of *Eriocaulon*, and the matter was further investigated by Holm (1904) in *E. decangulare*. The latter found that in this species the interruption, though often observed, was by no means constant and he pointed out that this is true also of other families in which it had previously been reported: for this reason he regarded this character as having little phylogenetic significance. There are no purely mechanical tissues in the root, but the diaphragms themselves are relatively rigid, while the intervening parenchyma is so soft and delicate that the epidermis sags inwards in these regions, emphasizing the vermiform appearance of the roots. Clearly this method of construction, while preventing collapse, imparts to the roots great flexibility. In the older parts of the root there are signs of disorganization and partial breakdown of the parenchymatous tissue between the diaphragms.

Chromosome number

The chromosome number of the present species has not yet been determined exactly, but preliminary counts made from metaphases in the cortical cells of root tips make it clear that the number is in the neighbourhood of 60. Very few other species of *Eriocaulon* have been investigated cytologically, but the chromosome numbers of three species are given by Darlington & Janaki Ammal (1945) on the authority of Erlandsson. They are as follows ($X = 8$ or 9): *E. cinereum*, 32; *E. truncatum*, 32; *E. sexangulare*, 36. Evidently, therefore, the present species is a higher polyploid. The significance of this fact will be referred to when the geographical distribution of the present species comes under review.

THE STRUCTURE OF *ERIOCAULON SEPTANGULARE* IN RELATION TO ITS ENVIRONMENT

In concluding this account of the morphology and anatomy of *E. septangulare* it will be of interest to consider the structure of the plant in relation to its aquatic environment. Clearly the species is markedly specialized; indeed, it is not possible to examine it in

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Text-figs. 34–40. Anatomy of the root. Text-fig. 34. Diagrammatic radial longitudinal section of the mature root, showing the disk-like diaphragms alternating with cylinders of parenchyma. (×44.) Text-fig. 35. Shows at higher magnification the portion of Text-fig. 34 enclosed by broken lines. (×125.) [*s.*, stele; sh_1 and sh_2, inner and outer sheaths; *d.*, diaphragm; *c.p.*, cortical parenchyma.] Text-fig. 36. Diagrammatic tangential longitudinal section through cortex of root. (×140.) Lettering as in Text-fig. 35. Text-fig. 37. A few cells of the diaphragm seen from above; the simplified outline of *d*, Text-fig. 38, has been used. Overlying cortical cells shown dotted. (×170.) Text-fig. 38. In right centre two cells of the diaphragm in accurate outline. (×400.) *a*, section along *AA*; *b*, section along *BB*; *c*, section along *CC*; *d*, simplified diagrammatic outline, as used in Text-figs. 37 and 39. Text-fig. 39. A section of a diaphragm in surface view shown diagrammatically, with the adjoining stele and its sheaths. 1 to 5, the concentric rings of diaphragm cells; *a* to *e*, diaphragm cells whose outer ends have bifurcated. (×125.) Text-fig. 40. Transverse section of the stele of a root showing pentarch structure and the protoxylem in contact with the endodermis. (×490.)

detail, or study its performance in the field, without recognizing how closely it is attune to the conditions which govern its life beneath the water. In endeavouring to interpre its structural peculiarities there is, nevertheless, an initial difficulty, for without resort t carefully controlled experiment it would not be possible to distinguish precisely betwee those features that are inherent in the genotype and those which may be due to th direct, phenotypic response of the individual to its environment. Long familiarity wit the plant in the field, coupled with observation of its performance under diverse condition in culture, has, however, revealed the fact that the present species is an unusually plasti one; both the external form and the internal structure of the individual plant can b modified to some extent by corresponding changes in the *milieu*. Some account of thes observations will be given in a subsequent paper and in the following discussion th salient structural features of *E. septangulare*, in its typical normal form, will be passe briefly in review without considering how they have arisen, and an attempt will be mad to relate them to the conditions under which the species grows in its natural habitat.

With its narrow, subulate leaves, grouped in a compact rosette, *Eriocaulon* has a habi of growth especially prevalent in those aquatic plants that grow rooted in the substratum beneath still water. *Littorella uniflora* and *Lobelia dortmanna*, frequent associate of *Eriocaulon* in the lochs of Ireland and the Hebrides, both resemble it in this respect while *Isoëtes lacustris*, though taxonomically so remote from it, provides a still mor striking parallel. Leaves of the type referred to are well adapted to withstand th fluctuating stresses set up by wave action, and it is perhaps significant that all the specie named inhabit the shallow margins of lochs and pools, where in stormy weather surfac movements can be quite severe. Plants with this habit of growth are not, however confined to such situations.

A much clearer correlation with environmental conditions is shown by the seedling which, it will be recalled, possesses a peculiar anchoring device which secures it to th substratum before the radicle appears, so counteracting its natural buoyancy and preventing it from rising to the surface of the water beneath which it germinates.

It is, however, in its internal structure that *Eriocaulon septangulare* provides th clearest evidence of accommodation to sub-aqueous conditions. This is seen perhaps mos clearly in certain peculiarities in the structure and disposition of its tissues, particularl those which are concerned: (*a*) with support, (*b*) with photosynthesis, and (*c*) wit aeration. These three aspects of its organization will be considered briefly in that order

(*a*) *Tissues concerned with support*

It may be well to emphasize here that the problem of support in submerged aquati plants differs in certain fundamental respects from that of terrestrial species. In th first place, the former are protected from the bending and torsional stresses occasioned b the wind, to which the great majority of land plants are exposed and to withstand which they must be adequately equipped. In the present species this is reflected not only in th absence of specialized mechanical tissues throughout the plant body but also in th unusual disposition of its vascular bundles. In all the organs of the plant, even those o axial nature, the vascular strands are grouped near the centre; in none of them does th usual peripheral series occur.

Although protected from the wind the plant is, as already noted, exposed to wav action and it is of interest to note that the parenchymatous tissues of the stem and lea and scape are so arranged that they provide in themselves the requisite degree of strength Thus, from the mechanical point of view, the leaf with its crescent-shaped cross-section its external corrugations and internal girder-like partitions is adequately stiffened, whil the scape with its alternating ridges and furrows, and its internal radial ribs, separate by circular canals, has a typical columnar structure. In this way both organs acquir sufficient strength, yet do so without sacrificing either lightness or flexibility. There ca be no doubt that a nice adjustment of these three complementary qualities makes for th success of the species in its life beneath the water; a fact which may be overlooked when it is grown in culture but which becomes clear enough when it is observed in its natural habitat. The behaviour of the inflorescence axis provides a rather striking illustration. This organ varies in length from a few inches when the plant is growing in shallow water to several feet when it is deeply submerged, and is so constructed that it achieves rigidity when short yet becomes perfectly flexible when long. The reactions of the two kinds to stormy weather are instructive. Whereas the short scapes withstand the shock of the wavelets on shallow shores and remain upright and unbending, the long ones in deeper water meet the menace of the larger waves not by resisting but by yielding to them, bending and straightening again as the waves approach and pass, yet all the while bearing aloft the capitula clear above the troubled water. Under the same conditions the flowers of *Lobelia Dortmanna,* borne on rigid stems, often become waterlogged.

A further consequence of submergence is the upward reaction of the water, which acts in opposition to the force of gravity. For *Eriocaulon septangulare* this upthrust exceeds the weight of the plant itself, which is in consequence subject to a resultant force acting upwards, not downwards as in all terrestrial species. With these conditions in mind the absence of mechanical tissues throughout the plant is natural enough, for no part of it has any weight to carry; yet at the same time the upthrust of the water may become a positive danger, since it tends to drag the plant from its moorings. We have already seen how this danger is met in the seedling by means of a special anchoring mechanism, but the mature individual is exposed to the same risk and in a later paper, dealing with the ecology of the species, it will be shown that the tendency to up-rooting sets a limit to the successful establishment of *E. septangulare* in certain habitats, which in all other respects are highly favourable to it.

(*b*) *Tissues concerned with photosynthesis*

The present species grows at depths beneath the water ranging from a few inches to over five feet, with the majority of individuals occurring within the range of one to three feet. The water is usually clear; nevertheless, some measurements made by the writer in the lochs of Skye confirm Pearsall's findings for the English lakes (1917), and show that the light intensity under water falls off rapidly with increasing depth below the surface; at a few feet it is reduced to a fraction of its value in the air above. If, then, the plant is to survive and flourish under these conditions it is clear that it must utilize to the full its capacity for photosynthesis, and certain peculiarities of its structure and organization are best explained in the light of this necessity. Thus we find that not only the leaf but also the spathe and scape are bright green and richly supplied with chloroplasts; each of these organs plays its part in carbon assimilation. The role of the scape merits special consideration: appearing in late spring it persists throughout the summer and autumn, when maximum demands are made on food resources, and is then discarded. Again, although the leaf rosette at soil level may be feebly illuminated beneath deep water, the scape at least reaches to the light; its upper, bright green portion, rising above the surface, where it is always well illuminated. Moreover, the scape has a compensatory action, for the more deeply submerged the plant, the larger the scape and the greater the part this plays in photosynthesis; hence, it must have a balancing effect on the total assimilation.

Passing to the internal structure of the leaf we find again signs of specialization. This is seen perhaps most clearly in the unusual disposition of its assimilatory tissues, which are arranged in two planes mutually at right angles. There is first a subepidermal layer of chlorenchyma beneath both faces of the leaf, forming a loose reticulum, with wide intercellular spaces. This renders the leaf markedly translucent and light penetrates it freely to fall on the series of transverse diaphragms, which at frequent intervals cross the air canals traversing the leaf from base to apex. These diaphragms, which in most aquatic plants are colourless, or nearly so, are in the present species bright green and richly supplied with chloroplasts; whatever other part they play their assimilatory role is patent The structural peculiarities of the leaf of *E. septangulare* recall the 'shade' type o organization and suggest equipment for efficient assimilation in low light intensities.

(c) *Tissues concerned with aeration*

Turning now to the problem of respiration, it is evident that the manner of growth of *E. septangulare* in dense colonies, rooted in finely divided silt beneath static water o considerable depth, creates conditions which demand adequate supplies of oxygen and effective provision for gaseous diffusion. The remarkable elaboration of its aerating system—perhaps the most striking feature of the anatomy of the species—seems clearly related to this demand. All the submerged parts of the plant are provided with intercellular spaces, but the character of the air spaces in the several organs varies and reflects their diverse functions and different environmental conditions. Thus for the root and rhizome, buried in waterlogged soil or creeping over its surface, the need for oxygen is most acute, and in these parts the aerenchyma exhibits small but very numerous intercellular spaces, so that the internal atmosphere bathes almost every cell outside the vascular tracts. For the leaf and spathe and scape, conditions are less severe and here we find wide longitudinal canals which facilitate the downward diffusion of oxygen. Once again the scape has a significant role, for it provides a channel of communication linking the oxygen-starved organs below with the well-aerated upper layers of the water. Eventually there is direct access to the air above, for the upper part of the scape, well provided with stomata, rises at length above the surface of the water. The diurnal cycle of gaseous exchange can be observed in a very direct way in the present species by a change in colour. During the day, and especially in bright sunlight, oxygen accumulates in the intercellular spaces, and the leaves and spathes then appear bright, glistening, silver-grey beneath the water. With the onset of darkness assimilation ceases, and during the night the oxygen is largely removed; partly perhaps by slow diffusion into the water, but there can be little doubt that most of it is directly utilized in respiration. The result is that with the returning light, the plant is seen to have lost its silver tinge and now appears a bright grass green.

Finally, the occurrence of stomata and hydathodes on the leaves of *E. septangulare* calls for comment. Both those structures might well be regarded as anomalous in a species which is fully, and often deeply, submerged beneath the water; nevertheless, they have been reported in several other plants of similar habitat. In some of these the stomata have been shown to be permanently closed, roofed over by the cuticle, or otherwise rendered non-functional and in all such instances they are doubtless vestigial; they suggest that for the species in question the aquatic habit is derived rather than primitive. In *E. septangulare* the stomata appear to be quite normally constituted, but the frequency of their occurrence on the leaves is so low that they can scarcely be of much significance, nor is it likely that they would lead to flooding of the tissues unless a strong negative pressure developed within the leaf.

On the scapes the stomatal frequency is much higher and steadily increases from the base of the organ to its apex. In terrestrial plants stomatal gradients of this kind are well known (see, for example, Zalenski, 1904; Yapp, 1912), and taken in conjunction with other anatomical gradients of a similar kind they have been regarded as indications of increasing xeromorphy; the distal portion of a leaf being farthest from the water-conducting tracts of the stem, while the upper leaves develop in an increasingly dry atmosphere. In a submerged aquatic plant such an explanation can hardly apply, since all the stomata are laid down and develop in a uniform and constant humidity; but however the gradient in stomatal frequency on the scapes of the present species may have come about, it would appear to have real significance. It will be recalled that the upper part of the scape (where the stomata are relatively abundant) emerges at length above the water, so that the stomata here have direct access to the air. Thus a diffusion gradient will be established in the wide longitudinal canals of the scape and the supply of oxygen to the submerged organs will be much facilitated. Throughout the reproductive phase, therefore, the scape provides a channel of communication linking the roots and rhizome of the plant, buried in waterlogged silt, with the open air above the water.

The hydathodes of *E. septangulare* closely resemble those reported by Sauvageau (1891) in *Potamogeton densus* and take the form of open pores at the leaf apices. The veins of the leaf converge towards this point, where the ultimate tracheids come into open communication with the surrounding water. The writer has found that if the water overlying growing specimens of the plant is lowered until the tips of the leaves just protrude the surface, and if the plants are then covered with a bell-jar, the familiar phenomenon of guttation is soon observed. Evidently there is a 'transpiration stream' throughout the plant, and since this must be maintained by the roots, the latter should not be regarded merely as a means of anchorage, but as actively absorbing organs. *E. septangulare* thus comes into line with other rooted aquatic plants in which a similar movement of water has been demonstrated (Arber, 1920, pp. 260–6).

Acknowledgements

The greater part of the work involved in this investigation was carried out at the University of Aberdeen, and I desire particularly to thank Prof. J. R. Matthews for his kindly criticism and advice: his interest in my work has been throughout a constant inspiration and encouragement.

I am also indebted to Sir Edward Salisbury and Dr C. R. Metcalfe, who kindly provided facilities for continuing the work at The Royal Botanic Gardens, Kew. Prof. J. McLean Thompson has given me every encouragement to complete the work at the University of Liverpool. I also acknowledge with gratitude a generous grant from the latter University towards the cost of illustrating the present paper.

Other friends and colleagues have helped me by supplying material and in various other ways, for which full acknowledgement will be made in a forthcoming paper dealing with the ecology and geographical distribution of *E. septangulare*.

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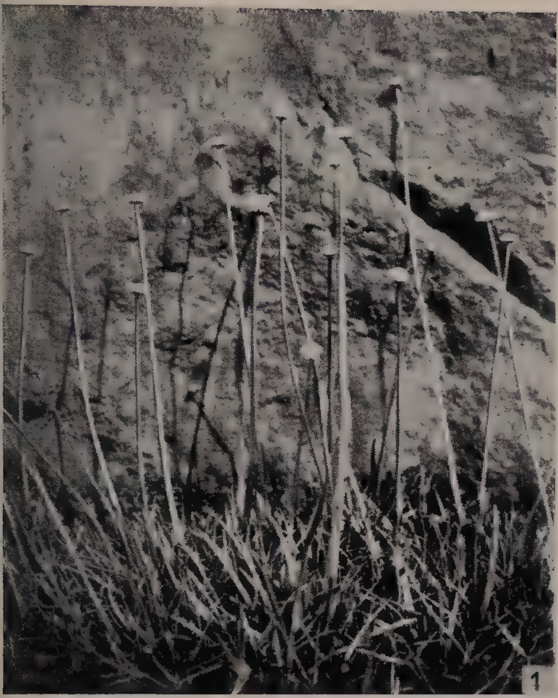
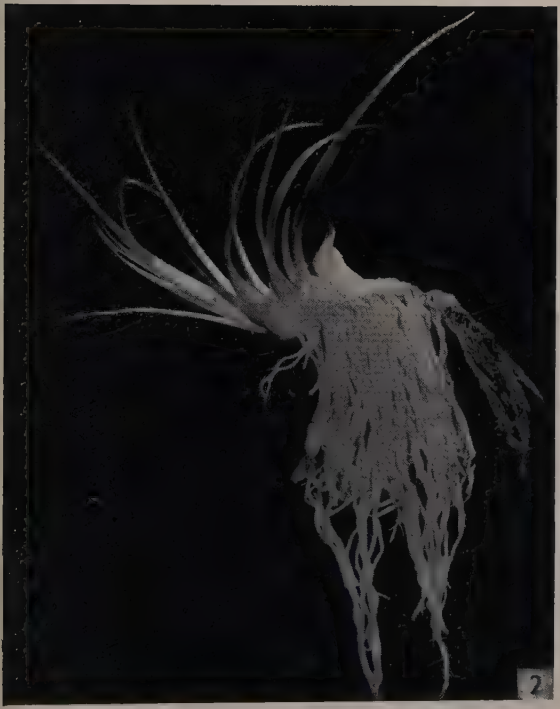
EXPLANATION OF PLATE 22

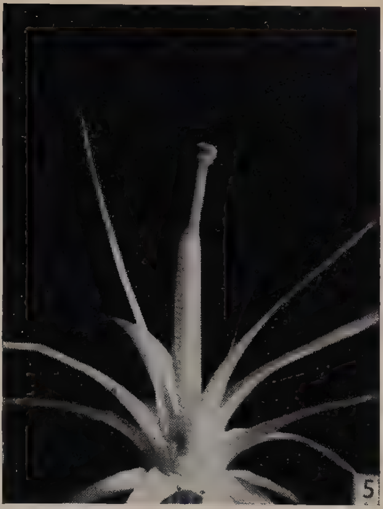
Fig. 1. Shows a small colony of specimens of *E. septangulare* at Cregduff Lough, Connemara, Ireland. (These are seen in the figure exposed above water after a period of drought.) This photograph, taken by Mr Welch, is reproduced by kind permission of the author and publishers, from Dr R. Lloyd Praeger's *The Botanist in Ireland* (Hodges, Figgis and Co.), Dublin, 1934.

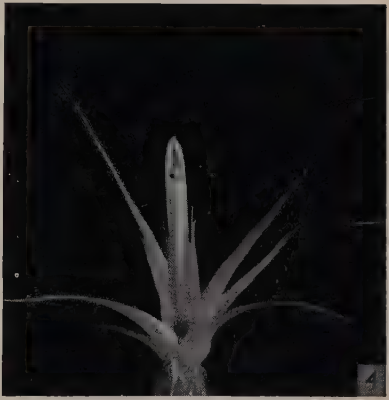
Fig. 2. An isolated specimen of *E. septangulare* which had been grown in culture at Aberdeen. (Actual size.)

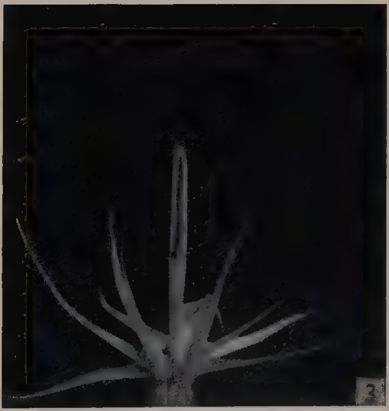
Figs. 3–5. Specimens selected to show stages in the growth of the spathe and scape. (Actual size.)











Eriocaulon septangulare **With.**

A contribution to the floral morphology and embryology of Dendrophthoe falcata (L. f.) Ettingsh.

By Bahadur Singh, Balwant Rajput College, Agra (India).

(With Plate 23 and 64 Text-figures)

(Communicated by C. R. Metcalfe, M.A., Ph.D., F.L.S.)

[Read 10 May 1951]

INTRODUCTION

The family Loranthaceae possesses many unique features, some of which are undoubtedly the result of a parasitic mode of life. There are others, however, which cannot be explained on this basis. The following investigation, which deals with the embryology of *Dendrophthoe falcata*, was undertaken at the suggestion of Prof. P. Maheshwari. He (1937, p. 375) writes that 'the Loranthaceae, Balanophoraceae, and Santalaceae are among the most difficult angiosperms for embryological investigation', and stresses the need for further studies on these families by botanists resident in the tropics.

REVIEW OF PREVIOUS WORK ON THE LORANTHOIDEAE

Changes in nomenclature. The nomenclature of the family has recently undergone considerable changes as the result of Danser's (1929) classification of the Loranthaceae of the Old World. The original genera, *Elytranthe* and *Loranthus* (Engler & Prantl, 1893, 1935), have been broken up into several new genera.

The following is a list of the older synonyms of the plant now known as *Dendrophthoe falcata* (L. f.) Ettingsh.: *Amyema pilosa* Dans., *Dendrophthoe bicolor* Mart., *D. indica* Miq., *D. curvata* Miq., *D. incarnata* Miq., *D. falcata* Ettingsh., *D. longiflora* Ettingsh., *D. vitellinus* van Tiegh., *D. odontocalyx* van Tiegh., *D. indicus* van Tiegh., *D. elegans* Dans., *D. leptopetala* Dans., *Elytranthe bleeseri* O. Schwarz., *Etubila longiflora* Rafin., *Leucobotrys pilosa* van Tiegh., *Lonicera zeylanica* Gaertn., *Loranthus falcatus* L. f., *L. longiflorus* Desr., *L. bicolor* Roxb., *L. curvatus* Bl., *L. koenigianus* Schult., *L. elegans* DC., *L. amplexifolius* DC., *L. incarnatus* Korth., *L. imbricatus* Edgew., *L. lineatus* Edgew., *L. vitellinus* F. V. Muell., *L. odontocalyx* Benth., *L. pilosus* Engl., *L. lauterbachii* K. Schum., *L. leptopetalus* Bl., *L. dolichoclades* K. Schum., *L. kerrii* Craib., *L. cambodianus* Lec., *L. aurantiacus* Ridl., *Scurrula longiflora* G. Don, *S. indica* G. Don, *S. elegans* G. Don, *S. bicolor* G. Don, *S. falcata* G. Don, *S. amplexifolia* G. Don, *S. koengianus* G. Don, *S. curvata* G. Don.

Embryology. Our knowledge of the embryology of the Loranthoideae is chiefly due to the works of Griffith (1838, 1844), Treub (1881, 1883*a*, *b*), Rauch (1936), and Schaeppi & Steindl (1942).

Griffith (1838, 1844) reported that in *Loranthus scurrula* L. (now *Scurrula parasitica* L.) and *Loranthus longiflorus* Desr. (now *Dendrophthoe falcata* L. f. (Ettingsh.)) there is a free-central placenta in the cavity of the ovary. He showed that the placenta is separated from the carpel wall by a free space and eventually grows into the stylar canal. Several embryo sacs are formed in the stylar canal, and the pollen tubes entering these embryo sacs give rise to embryos which elongate considerably so as to reach the ovary.[1]

Treub (1881, 1883*a*, *b*) worked on *Loranthus sphaerocarpus* Bl. (now *Macrosolen cochinchinensis* (Lour.) van Tiegh.) and *Loranthus pentandrus* L. (now *Dendrophthoe pentandra* (L.) Miq.). According to him the tip of the floral axis grows into the cavity of the ovary, and the embryo sacs are formed inside a structure called the 'mamelon', whose exact morphological nature he was unable to clarify.

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[1] Griffith evidently believed in the old pollen tube theory of Schleiden according to which the pro-embryo arose from the tip of the tube and not from the egg.

Regarding the development of the female gametophyte in *Macrosolen cochinchinensis*, Treub states that the megaspore mother cells divide to form rows of three cells, of which the uppermost functions to form an embryo sac. No antipodal cells were seen in the mature embryo sac, there being only a single free nucleus in its lower half. In *Dendrophthoe pentandra* Miq. only five to eight embryo sacs are formed, six to seven being the usual number. The first division of the fertilized egg is vertical, and the subsequent divisions are transverse thus giving rise to a biseriate pro-embryo.

The recent papers on the subject are by Rauch (1936) and Schaeppi & Steindl (1942). In *Scurrula atropurpurea*, Rauch finds a narrow stylar canal which widens only slightly at the bottom to form the cavity of the ovary, but in *Dendrophthoe pentandra* the cavity is slightly wider. In both cases the hypodermal cells at the base of the ovary differentiate into an archesporium which becomes more deep seated in older stages. The cells of this tissue elongate considerably and form the megaspore mother cells which are almost spindle-shaped, and divide to form rows of three cells of which only the topmost functions. The embryo sacs elongate considerably and protrude into the stylar canal, reaching approximately up to its middle. The basal ends of the embryo sacs grow down as far as the pad of collenchymatous cells which is differentiated slightly above the bottom of the ovary. Double fertilization occurs. One synergid is always destroyed by the pollen tube but the other persists for a while, being recognizable even when the pro-embryo has attained considerable length. The endosperm, which is of the cellular type, begins to develop at an early stage, starting at the base of the embryo sac and gradually extending upward. The embryo develops much later. The first division of the egg is longitudinal, and is followed by several transverse divisions resulting in a long biseriate pro-embryo which gradually pushes its way down from the style into the ovary. The two terminal cells of the pro-embryo form the embryo proper. Although a number of embryos are initiated, only one develops to maturity. This is nourished by a common nutritive mass formed by the fusion of the endosperms of several embryo sacs.

Schaeppi & Steindl (1942) have studied nine genera and fourteen species of the Loranthoideae. They find some plants with a distinct placenta in the ovary (*Lepeostegeres gemmiflorus*, *Macrosolen cochinchinensis*, *M. formosus*, *M. pseudoperfoliatus*, *Elytranthe parasitica* and *Amyema gravis*), and others without it (*Helixanthera hookeriana*, *Brathranthus axanthus*, *Dendrophthoe pentandra*, *Scurrula atropurpurea* and *Taxillus tomentosus*). The development of the embryo sac is of the normal type, but the height to which the sac reaches differs a good deal in different genera. In *Macrosolen* the egg apparatus is seen somewhere near the junction of the style and ovary; in *Elytranthe* above the transition of the ovary into the style; in *Lepeostegeres* in the lower one-fourth of the style; in *Amyema* at the middle; in *Taxillus* somewhat above the middle; and in *Helixanthera* in the stigmatic region just below the papillate layer. The antipodals organize into three ephemeral cells in *Lepeostegeres gemmiflorus*. In *Macrosolen formosus* two degenerated cells were seen in the antipodal end, while in *M. cochinchinensis*, *M. pseudoperfoliatus*, *Helixanthera hookeriana*, *Taxillus tomentosus* and *Dendrophthoe pentandra* no antipodals could be identified.

GEOGRAPHICAL DISTRIBUTION

The genus *Dendrophthoe* is distributed over a large area, ranging from tropical Africa in the west to the Solomon Islands in the east (Danser, 1935*b*). In India it is found from the River Jhelum eastwards in the sub-Himalayan tracts in Kumaun to a height of 7500 ft. above sea-level (Brandis, 1906; Hooker, 1890; Gamble, 1922). It is common in Bengal, Central India, Utter Pradesh, Bihar, Orissa, and in the Madras and Bombay presidencies. Five species of the genus occur in the Philippine islands (Danser, 1935*a*, p. 108). It also occurs in Ceylon and the western parts of the Malaya Archipelago, the number of species in this area being larger than those in the eastern part. In Celebes there is only one species, *D. falcata*, which extends into the north-western parts of New Guinea and tropical Australia, Siam and Burma. As far as the author is aware, the genus is not found in America.

This wide distribution is difficult to explain. Danser (1931) states that owing to the baccaceous nature of the fruit, and the viscous mesocarp, the chances of distribution of seeds of the Loranthaceae by man, storms, or sea currents, etc., are 'well-nigh impossible'. According to Ridley (1930), the seeds are chiefly disseminated by birds. G. M. Ryan (1899)[1] reports that he saw a common squirrel eating the pulp of the berries and discarding the seeds practically uninjured. I have seen small birds visiting the plants and passing the seeds out of the alimentary canal. Sometimes a series of seeds was seen, attached to one another like a string of beads, suggesting that they were ejected in quick succession.

MATERIAL AND METHODS

The material for the present study was collected from Lucknow, Kanpur, Meerut, Allahabad, Bareilly and Cuttack from the following hosts: *Melia azedarach*, *Azadirachta indica*, *Mangifera indica*, *Ficus religiosa*, *Mimusops elengi*, *Ficus benghalensis*, *Anona squamosa* and *Eriobotrya japonica*. The collections from Meerut and Bareilly were made by my friends Drs V. Puri and B. M. Johri. Dr A. K. Mitra sent me some material from Allahabad, and at the beginning of my studies I had the advantage of examining some slides of the ovary and stamens kindly given to me by Dr P. Maheshwari and Mr H. R. Bhargava.

The following fixatives were used: Nawaschin's fluid, 'Craf', Carnoy's fluid, Allen's modification of Bouin's fluid, and formalin acetic alcohol. The best results were obtained with Nawaschin and Craf. As the material passed through xylol became rather brittle, other dehydrating and clearing agents were tried, namely, cedar oil, chloroform, normal butyl alcohol, glycerin and dioxan. Of all these, normal butyl alcohol and dioxan proved to be the most satisfactory.

For fixing the ribbons to the slides a mixture of 'gloy' and potassium dichromate was used in the beginning. But this did not prove satisfactory with sections of the style, which became detached from the slides in the lower grades of alcohols, although other parts of the flower were held perfectly. Meyer's egg albumen and Haupt's gelatin fixative also proved unsuccessful with sections of the style. Slightly better results were obtained by using a combination of Meyer's egg albumen with gloy and potassium dichromate. The egg albumen was spread on the slide in a thin film with a finger. A dilute solution of gloy and dichromate in water was then poured on to the slide. The ribbons were floated on this solution and then expanded on a warm plate in the usual manner. The excess fluid was drained off and the slides left in diffuse light for at least 2 hr.

Sections were cut 5–40μ thick depending on the purpose in view and stained with iron-alum haematoxylin differentiated with picric acid, Newton's crystal violet and erythrosin, and crystal violet and orange G.

Owing to the length and curvature of the style longitudinal sections of the entire pistil required a special technique. The styles had to be straightened before sectioning. This was done after embedding them in paraffin by the following method. The entire block was placed in warm water for a few minutes. The paraffin which became softened was gradually bent to the desired plane in order to straighten the pistil embedded inside it. After each treatment the block was placed under cold water in order to harden the paraffin and set the pistil in its new position. The warming, bending and cooling were repeated until the pistil was completely straightened. Crude though this method appears to be, it was of special advantage in obtaining entire sections of the style so that the embryo sacs could be traced from top to bottom.

For the germination of the pollen grains a 1% solution of agar with varying amounts of sugar was spread in thin films on the slides (Maheshwari & Wulff, 1937). After dusting the pollen grains the slides were put in a moist chamber. The best germination was obtained with 15 % cane-sugar. The slides were dipped in weak Fleming's fluid to kill and fix the pollen tubes.

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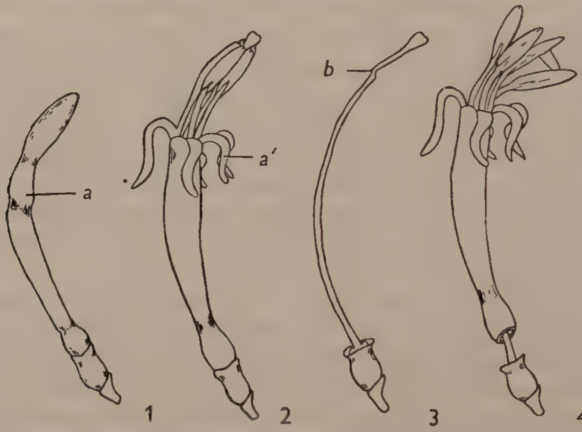
[1] As cited in Fischer (1926).

THE FLOWER

External morphology. The perianth is formed of five, rarely four, members fused to form a tube of orange yellow colour, lying within a five-toothed 'calyculus' whose morphological nature is still in dispute. In a mature flower the perianth tube measures from 45 to 50 mm. in length, narrow below and widening very gradually towards the upper part. Shortly above the middle region it shows a constriction, followed by a swollen band (*a*) of greenish yellow colour (Text-fig. 1). Above this bend the five perianth lobes join together to form a pointed bud, but become sharply reflexed (*a′*) when the flower opens (Text-fig. 2).

The stamens are epiphyllous, with the filaments adnate to the perianth for some distance. The basifixed anthers, closely pressed round the style in the bud condition, are nearly as long as the free parts of the filaments. The two outer sacs of the anther are slightly longer than the inner ones. Schaeppi & Steindl (1942) report the same in the anther of *Scurrula atropurpurea.*



Text-figs. 1–4. Flowers and buds at different stages of growth (*a* = swollen part of perianth tube; *a′* = reflexed tips of perianth lobes; *b* = bend in the style). Text-fig. 1. Flower bud before opening. Text-fig. 2. Open flower. Text-fig. 3. Pistil at the time of pollination. Text-fig. 4. Flower showing perianth hanging round the style for some time after fertilization. × Natural size.

Inside the perianth tube are five cushion-like nectaries which surround the base of a long, narrow, and somewhat curved style, 40–45 mm. long in adult flowers. The upper part of the style, 5–7 mm. long, frequently shows a reddish tint, while the remaining part is yellow. Some flowers show a conspicuous bend (*b*) in the style at the junction of the two colours (Text-fig. 3), while in others it is either inconspicuous or absent. The stigma is knob-like and bifid.

When the flowers are mature the perianth gets detached from the top of the ovary (Text-fig. 4), but remains hanging round the distal part of the style in the region of the bend. The final fall of the perianth is frequently accompanied by a shedding of the 5–7 mm. long distal part of the style, the rest of the style being shed at a slightly later stage.

The ovary is inferior and matures into an ovate pseudoberry, 5–11 mm. long and 6–8 mm. broad.

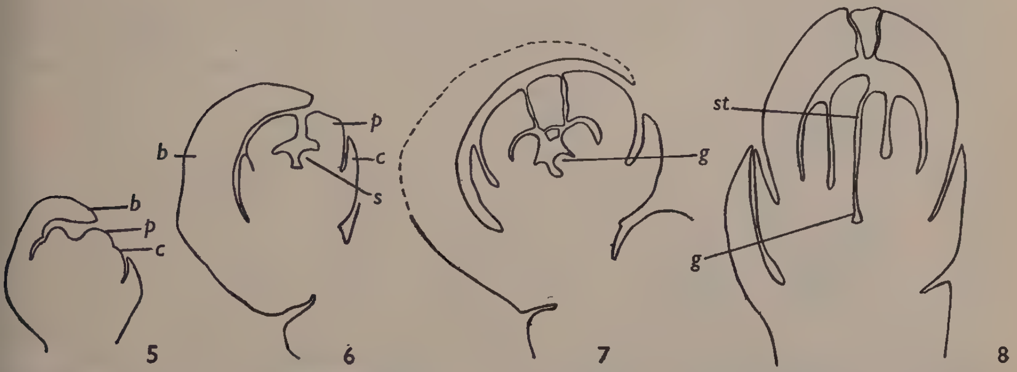
Organogeny. The primordium of the flower appears in the form of a small protuberance in the axil of a young bract (Text-fig. 5 *b*). From longitudinal sections of young racemes it was found that the floral parts arise in acropetal succession: calyculus, perianth, stamens and carpels.

Initially the calyculus is inferior in position (Text-fig. 5, *c*), but before the perianth is advanced in growth the torus stops growing and the staminal primordia (Text-fig. 6, *s*) are laid down at the same level as those of the perianth (*p*). The stamens begin to elongate as soon as the carpels make their appearance.

At the time the primordia of the gynaecium are laid down (Text-fig. 7) the ovary is seen to be at about the same level as the place of origin of the perianth. However, it soon becomes inferior in position to the other floral organs (Text-fig. 8). The calyculus forms a membranous ring on the top of the ovary. The stamens are adnate to the perianth for approximately four-fifths of their length, their upper parts alone being free.

There is a wide stylar canal (Text-fig. 8, *st*) which persists in later stages of development. The wall of the style is composed of greatly elongated and thin-walled cells.

The cavity of the ovary is fairly broad in the beginning, but it is totally obliterated in later stages. Ovules in the usual sense are absent.



Text-figs. 5–8. L.S. young buds showing primordia of bract (*b*), calyculus (*c*), gynaecium (*g*), perianth (*p*), stamens (*s*), and stylar canal (*st*). ×46.

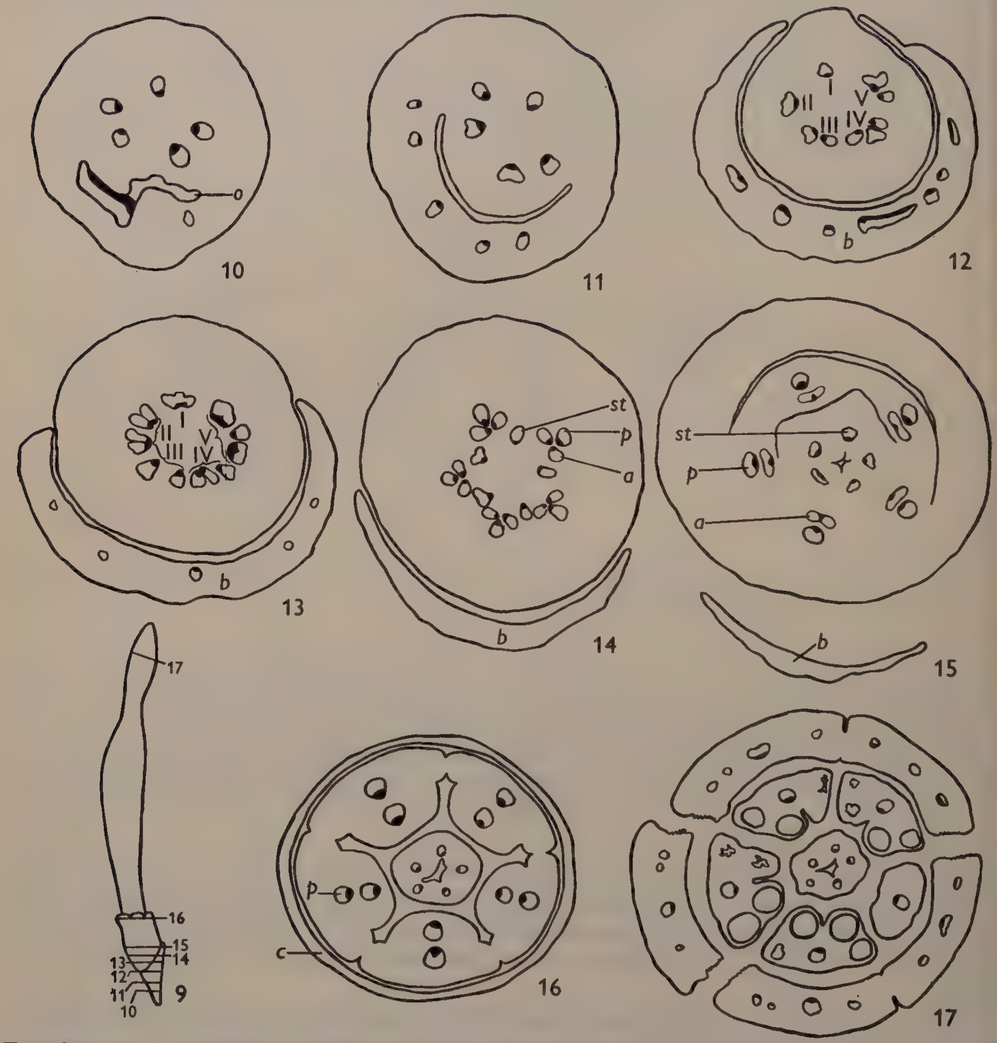
Vascular anatomy. The vascular supply of the flower was traced by means of serial cross-sections cut from below upwards. Text-figs. 10–17 show the structure as seen in transverse sections cut at the levels marked in the index figure 9.

The supply to the subtending bract begins as a single strand *o* (obliquely cut in Text-fig. 10) which branches into five to eight bundles in the free part of the bract (Text-figs. 11, 12). The apical part of the bract is, however, devoid of any vascular tissue (Text-figs. 14, 15).

After the supply to the bract has departed, the base of the flower is left with a ring of five bundles (Text-figs. 10, 11), each of which divides into three subequal strands, one median and two lateral. The five median strands enter the style and pass into the stigma where they divide to form as many as ten or sometimes only six to seven vascular traces.

The mode of division of the original five bundles, present at the base of the flower, can be understood by a reference to Text-figs. 12 and 13. In Text-fig. 12 bundle I is undivided, II shows signs of the beginning of a division in its phloem region, III and V have already formed two traces each one of which shows a bifurcated phloem, and IV has completed its division into three traces. In Fig. 13, which represents a section cut at a slightly higher level, bundles II, III and V have also divided into three vascular traces each, while I has just begun to divide. One of the lateral traces of II is in close proximity to a lateral trace of III, suggesting possible fusions of the adjacent lateral traces. These fused products divide again, however, so that besides the inner ring of five vascular traces (*st*) which supply the style, the ovary has fifteen other traces arranged in groups of three each (Text-fig. 14).

The two lateral traces of each group, which lie facing each other when just formed (Text-fig. 14), fuse to form a single collateral bundle with its xylem pointing inwards (Text-fig. 15). This newly formed ring of five bundles (Text-fig. 15) is destined to supply the androecium, one bundle entering each stamen. No change occurs in the number of the staminal traces, but the phloem which was previously extended tangentially now becomes rounded in outline so that the staminal traces acquire the same form as the outer traces which are really the median bundles of the triplets seen in Text-fig. 14.



Text-figs. 9–17. Text-fig. 9. Index figure to show levels at which the cross-sections 10–17 have been cut. × 2. Text-figs. 10–17. Cross-sections of flower showing vascular supply to various organs. For explanation see text. (*a* = staminal trace; *b* = bract; *c* = calyculus; *o* = vascular bundle going into bract; *p* = perianth trace; *st* = stylar bundle. × 23.

The median bundles mentioned above supply the perianth. Soon after the separation of the staminal filaments from the perianth, each bundle divides to form three to five traces (Text-fig. 17) which end just below the extreme tip of the perianth.

It is noteworthy that the calyculus receives no vascular supply whatever. Schaeppi & Steindl (1942) also find the same in the other members of the Loranthoideae studied by them.

As already mentioned, some flowers possess only four perianth lobes and the same number of stamens. In such cases the entire vascular supply of the flower is based upon a tetramerous instead of a pentamerous plan.

MICROSPOROGENESIS

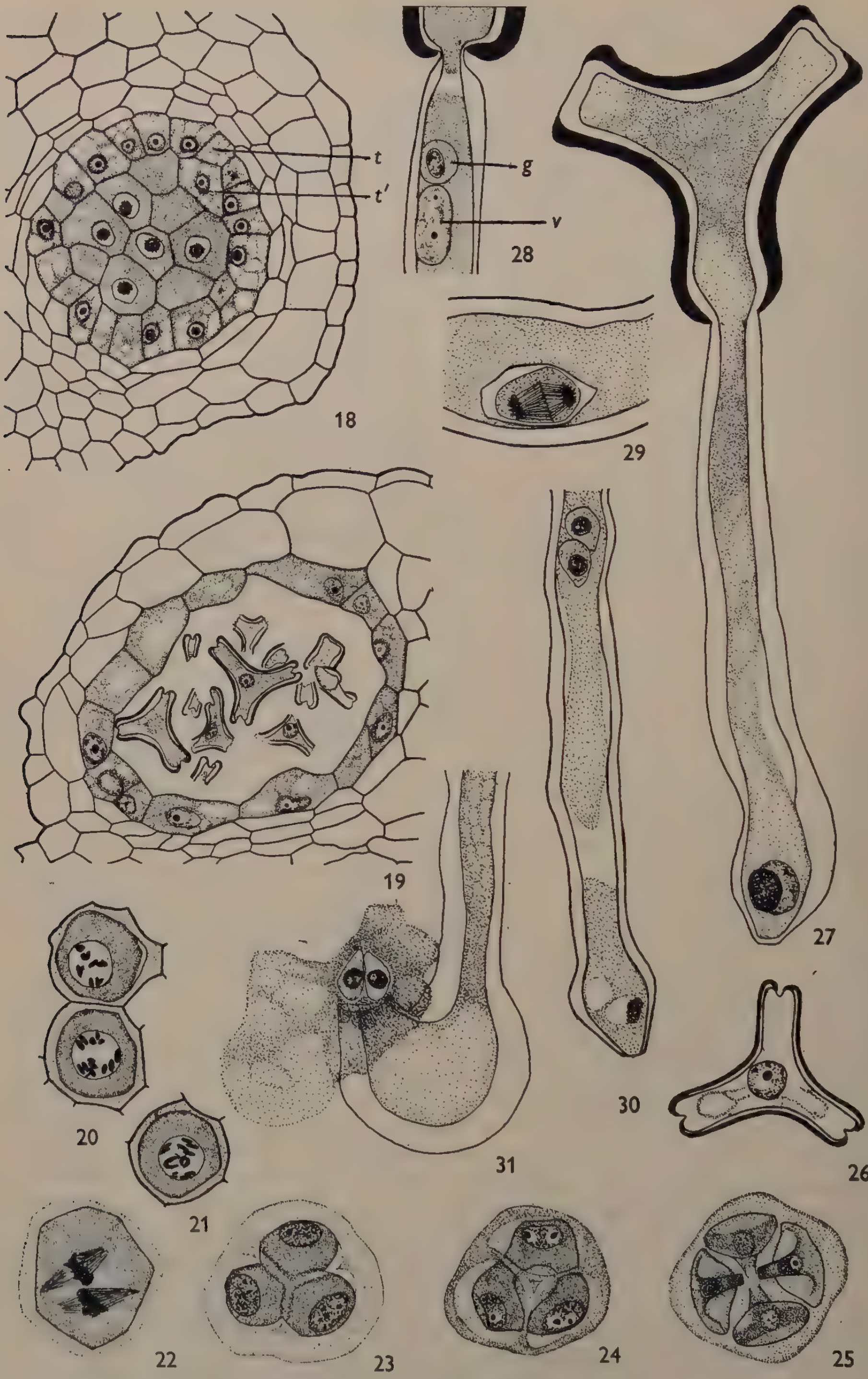
A transverse section of the young anther shows that the anther wall consists of the epidermis, endothecium, two middle layers, and a single-layered tapetum (Text-fig. 18). The middle layers are the first to degenerate, and are no longer distinguishable in anthers showing young microspores (Text-fig. 19).

In contrast to the condition in most angiosperms the cells of the tapetum remain uninucleate throughout their life (Text-figs. 18, 19). This is also the case in certain other members of the Loranthaceae, viz. *Phoradendron villosum* and *P. flavescens* var. *macrophyllus* (Billings, 1932), *Scurrula atropurpurea* and *Dendrophthoe pentandra* (Rauch, 1936). Only in *Scurrula* a few binucleate cells have been seen at places (Rauch, 1936). In *Korthalsella dacrydii* (Rutishauser, 1935) and *K. opuntia* (Rutishauser, 1937), on the other hand, the tapetum is always binucleate. According to Pisek (1923) there is no tapetum in *Viscum album*, but Steindl (1935, p. 347) notes that the innermost of the wall layers is composed of cells with several nuclei which are much larger than the nuclei of the vegetative cells. When dealing with *V. articulatum* he writes, however: 'Wie bei *Viscum album*, wird auch hier keine Tapetumschicht gebildet, die Pollenkammern liegen direkt im parenchymatischen Gewebe eingebettet.' This statement is in contradiction to the first, since the innermost wall layer with multinucleate cells could hardly be anything other than the tapetum.

I occasionally saw two layers of tapetum-like cells at certain points in the anther (Text-fig. 18, *t*, *t′*). One of Pisek's figures (fig. 3) of *Loranthus europaeus* Jacq. (now *Hyphear europaeum*) also shows a similar feature, although he does not call attention to this in the text. Since I did not come across any periclinal divisions in the tapetum, it is possible that such an appearance may be caused by the sterilization of a cell of the sporogenous tissue situated near the tapetum. In longitudinal sections these sterile cells often appear at regular intervals. Such a tendency if carried further would lead to the formation of transverse partitions in the anther, as seen in some of the Mimoseae. Schaeppi & Steindl (1942) have actually noted the presence of partition walls in the anther loculi of *Elytranthe parasitica* and *Amyema gravis*, but they do not describe the exact method by which these septa arise. Billings (1932) mentions that in *Phoradendron villosum* some of the mother cells degenerate and serve a tapetal function.

As an anther grows in age and size the tapetal cells enlarge and become vacuolate. After the reduction divisions are over they show distinct signs of degeneration. This is in agreement with Rutishauser's (1935) observations on *Korthalsella dacrydii*. When degeneration sets in, the tapetal nuclei stain more darkly and their cytoplasm shrivels up. In some cases they became amoeboid and are found to wander inside the loculus, but a true periplasmodium, as has been reported in some members of the family, e.g. *Arceuthobium*, *Phoradendron* and *Hyphear* (Steindl, 1935), could not be seen in my material. At the microspore stage dark globules were seen in the region of the tapetum in slides stained with iron-alum haematoxylin, and similar globules were identified over the thickened walls of the microspores. But after the thickening of the microspore wall is completed, the globules are no longer distinguishable. Ubisch (1927) found similar globules in *Oxalis rosea* and thinks that they contribute to the thickening of the microspore wall. The above observations on *Dendrophthoe falcata* seem to support this conclusion, although the exact method by which the thickening is brought about is not clear.

The cells of the endothecium enlarge and frequently show a resin-like substance at the microspore tetrad stage. When the pollen grains are binucleate they develop the usual fibrous thickenings. Meanwhile, the cells of the epidermis degenerate and disappear so that the endothecium becomes the outermost layer of the anther. Stevenson (1934) reports



Text-figs. 18–31. For legends see p. 457.

the same in *Korthalsella salicornioides* and *K. lindsayi*.[1] In *Hyphear europaeum* (Pisek, 1924), *Korthalsella dacrydii* (Rutishauser, 1935), *Dendrophthoe pentandra*, *Scurrula atropurpurea* (Rauch, 1936), *Korthalsella opuntia* and *Ginalloa linearis* (Rutishauser, 1937), however, the epidermis seems to persist even in the mature anther.

Johnson (1888, 1889), Heinricher (1915), Staedtler (1923), Pisek (1924) and Dowding (1931) report that in *Arceuthobium oxycedri* the epidermis itself acquires fibrous thickenings and functions as an endothecium. This deserves confirmation for it is possible that an epidermis is present in the younger stages. This has been clearly demonstrated in *Struthanthus calobotrys* by Goebel (1933), who states: 'Bei *Struthanthus* z. B. sitzen wie Fig. 2046, 6 zeigt, zwischen den Endotheziumzellen (die durch die fäserige Wandverdickung hervortreten) nur kleine, vereinzelte Reste der Epidermiszellen. Die Epidermis wird noch normal angelegt, später aber durch das Wachstum der Endotheziumzellen vielfach von ihr nicht mehr überlagert werden (Fig. 2046, 6).'

The microspore mother cells are formed by one or two divisions of the sporogenous tissue. They are distinguished from the tapetal cells by their lighter staining and slightly larger size. The walls begin to round up as soon as the cells enter upon the first phase of reduction division. At the same time a mucilaginous substance (Text-figs. 20, 21) appears between the cytoplasm and the wall, starting at the corners and then spreading to the sides. Similar observations have been made on *Korthalsella dacrydii* (Rutishauser, 1935), *Scurrula atropurpurea* and *Dendrophthoe pentandra* (Rauch, 1936), but the authors do not mention whether the original mother cell wall becomes mucilaginous, or the mucilage appears between the cytoplasm and the wall. Although the wall is very thin and inconspicuous at this stage, I was able to distinguish it in slides stained with Delafield's haematoxylin, and in many cases traces of it could be seen till the end of the reduction division. After this it gradually disappears, leaving only the mucilaginous coating round the tetranucleate mother cell (Text-figs. 22, 23).

The divisions of the microspore mother cells are simultaneous and the spindles of the second reduction division may be somewhat parallel, almost at right angles, or obliquely oriented with respect to each other (Text-fig. 22). Only tetrahedral (Text-figs. 23, 24) and decussate (Text-fig. 25) types of tetrads are seen. However, a tetrahedral tetrad, on being rotated by slightly pressing the cover-glass, looks like a decussate one, and vice versa. Rauch (1936) also figures two types of tetrads in *Scurrula atropurpurea* and *Dendrophthoe pentandra*, but makes no mention of the fact that the same tetrad may be called tetrahedral if viewed from one side and decussate when viewed from another.

In *D. falcata* the spindles of the first reduction division disappear before the second reduction division begins. The spindles of the second reduction division also disappear soon after meiosis is completed, but six secondary spindles soon arise and occupy the places of the primary spindles.

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[1] See also Mekel (1935).

Text-figs. 18–31. Stages of micro-sporogenesis and development of male gametophyte. Text-fig. 18. T.S. part of anther at microspore mother cell stage; note two-layered tapetum at *t*, *t′*. ×475. Text-fig. 19. T.S. anther at microspore stage; the middle layers have disappeared. ×475. Text-figs. 20, 21. Microspore mother cells in diakinesis; a mucilaginous substance has appeared between the cell wall and the cytoplasm. ×850. Text-fig. 22. Metaphase of second reduction division with obliquely oriented spindles. ×1015. Text-figs. 23, 24. Quadripartition of mother cells by centripetally advancing furrows. The wedges from the mucilaginous wall (Text-fig. 24) have united in the centre to form a swollen mass. ×1015. Text-fig. 25. Decussate tetrad. ×1015. Text-fig. 26. Microspore showing exine and intine; note the three germ pores. ×1015. Text-fig. 27. Germinating pollen grain showing densely stained generative nucleus and lightly stained vegetative nucleus. ×1015. Text-fig. 28. Part of pollen tube showing generative cell (*g*) and vegetative nucleus (*v*). ×1015. Text-fig. 29. Generative cell in telophase. ×2020. Text-fig. 30. Part of pollen tube showing sperm cells and degenerating vegetative nucleus. ×1015. Text-fig. 31. Burst end of pollen tube with two sperm cells lying in the extruded cytoplasm of the tube. ×1015.

Quadripartition of the mother cells takes place by six furrows originating at the periphery between the different nuclei (Text-fig. 23). As these furrows advance, they are followed by wedges of the mucilage wall which meet in the centre so as to cleave the mother cell into four parts.

The mucilage wall lying between the different microspores undergoes much thickening which is especially well marked in the centre (Text-fig. 24). Here we see a small spherica ball of mucilage which is connected with the outer mucilaginous layer by six strips of the same material whose middle portions are swollen to form six cylindrical connexions between the central ball and the outer mucilage. These connexions become slightly narrower towards the periphery.

MALE GAMETOPHYTE

Each microspore has a 3-rayed outline with concave sides and blunt apices, such as might be cut out of a concavo-convex discus. During maturation the usual exine and intine are formed, and, instead of remaining concavo-convex, the cells become double convex.

The pollen grains have a smooth and uniformly thick exine (Text-fig. 26) with three germ-pores. Rauch (1936) states that in *Scurrula atropurpurea* and *Dendrophthoe pentandra* the exine becomes somewhat thinner towards the arms.

The mature pollen grains are two-celled. As they are full of dense contents, it is very difficult to observe the nuclei.[1] Wefelscheid (1911) states that in *Viscum album* the generative nucleus is provided with its own cytoplasm and the entire cell moves from its original position near the wall of the pollen grain to its middle.

No germinating pollen grains were found on the stigma, but some pollen tubes could be seen inside the stylar canal. Wulff (1935) reports that in *Narthecium ossifragum* pollen tubes grown in culture are five to seven times broader than those in the style, but in my material both were of approximately the same width.

The generative nucleus divides after it has entered the pollen tube (Text-figs. 27, 28). Schürhoff (1922) and Steindl (1935) state that in *Viscum album* the generative cell divides while it is still in the body of the pollen grain, although germination has taken place and the pollen tube has reached an appreciable length.

When the generative cell of *Dendrophthoe falcata* enters the tube its nucleus is deeply stained and the cytoplasmic sheath around it is quite clearly seen (Text-fig. 28). The division of the generative cell begins after it has travelled quite a long distance into the tube. Text-fig. 29 shows the generative cell in telophase with very clear spindle fibres.[2]

The details of cytokinesis were not very clear in my preparations, but a cell plate is doubtless formed at the equatorial region. The sperm cells are spindle-shaped or oval, but the nucleus is in most cases quite spherical (Text-figs. 30, 31). One pollen tube in the stylar canal also gave a good view of the two ovoid sperm cells each with a distinct hyaline cytoplasmic sheath.

The vegetative nucleus (Text-fig. 27) is larger than the generative, and usually precedes the generative cell in the pollen tube. It stains very feebly and frequently presents a shrivelled and degenerated appearance (Text-fig. 28). In some pollen tubes it could not be seen at all. Apparently it increases in size, becomes less chromatic, and finally breaks up and disappears.

Some of the pollen tubes in my cultures were devoid of nuclei, and on examining the pollen grains from which these tubes were given out I found only one nucleus inside each of them. Apparently this was the undivided microspore nucleus which does not enter the pollen tube.

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[1] See Maheshwari (1949, p. 15, footnote 18).

[2] Some authors have reported that the division of the generative cell is characterized by an absence of spindle fibres, but careful studies made during recent years on a variety of material have always demonstrated their presence. Johnston (1941) recommends that for this purpose Delafield's haematoxylin is superior to Haidenhein's iron-alum haematoxylin. See also Maheshwari (1949).

The vegetative nucleus was always found in front of and close to the generative cell when the latter has entered the pollen tube.

A degeneration of the contents of the anther loculus is of frequent occurrence, and is commonest at the microspore mother cell stage. Some of the anther lobes become quite empty on account of the wholesale breaking down of the sporogenous tissue. The tapetal cells generally remain intact for a longer period, although eventually they also meet the same fate. Sometimes degeneration may start before the mother cell stage, but even in such cases the first sporogenous cells to degenerate are always those situated in the centre of the loculus. Billings (1932) also found a complete degeneration of the archesporial tissue in some anthers of *Phoradendron flavescens* var. *macrophyllum*, while other anthers showed fewer degenerating mother cells.

In *Dendrophthoe falcata* degeneration of the microspore mother cells is so widespread that hardly 20 % of the anthers show a perfect development of all the loculi. Anthers with one degenerating loculus are especially common. In some very young flowers all the anthers were found to have dried up, but such an extreme condition is very rare in older stages. This suggests that flowers, of which all the anthers degenerate, soon wither.

A degeneration of the microspore tetrads, microspores and binucleate pollen grains is also frequent. In *D. pentandra* also, according to Rauch (1936), a large number of the pollen grains are shrunken and remain sterile.

It may be added that frequently the microspore mother cells situated at the apex of an anther continue their development, while the rest of the anther becomes quite hollow.

MEGASPOROGENESIS

As the place of origin of the female gametophyte is unusual and its further development s also of an aberrant type the entire course of events is diagrammatically represented in Text-fig. 32. Along with each diagram there is also shown a flower approximately of the age at which that particular stage occurs.

Text-fig. 33 represents a longitudinal section cut through the basal part of the ovary cavity. The hypodermal cells and frequently a few other cells, situated in the second and third layers, develop archesporial characters. Their nuclei become larger and the cells stain more densely than the cells of the surrounding tissue. Just after the differentiation of the archesporial tissue, cells situated near the bottom of the ovary become collenchymatous and form a prominent pad which is characteristic of all the members of the family so far nvestigated. In *Dendrophthora*, belonging to the subfamily Viscoideae, a pad of tracheids s formed instead of the collenchyma (York, 1913*a*, *b*). In *Dendrophthoe falcata* the pad has the shape of a shallow cup. Some three or four layers of cells above it remain thin-walled and stain very lightly.

The archesporial cells sometimes undergo one or two divisions, but no parietal cells are cut off and the cells formed as a result of such divisions function as megaspore mother cells Text-fig. 34, and Pl. **23**, fig. 1).

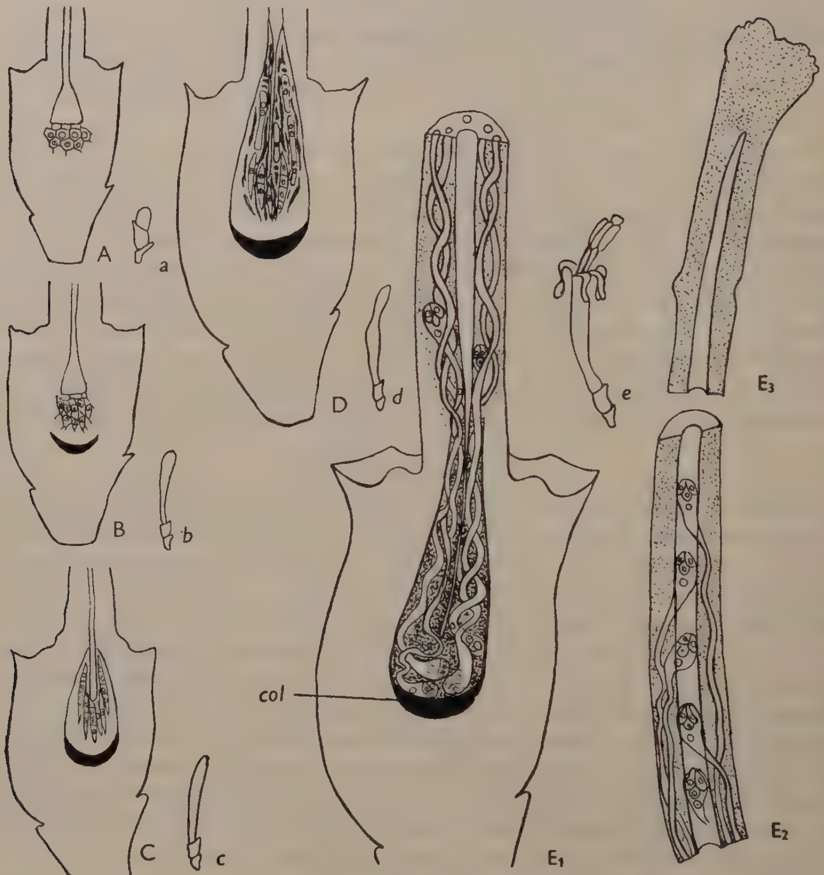
FEMALE GAMETOPHYTE

The megaspore mother cells elongate very markedly and become more or less spindle-shaped (Text-fig. 34). The nucleus of a mother cell lies either in the lower part of the cell r in its centre. It is only rarely that it is found in the upper part.

The tissue surrounding the megaspore mother cells is parenchymatous. The cells longate considerably, and since their walls are very thin, material of this age is easily uptured during section-cutting.

Some of the mother cells elongate but do not divide; a few take a dark stain and show igns of degeneration; and still others do not degenerate but are arrested in growth. The longated mother cells glide up along the inner epidermis of the ovarian cavity (Text-g. 35) which becomes narrower and narrower and is finally completely obliterated cf. Rauch, 1936).

The functioning megaspore mother cells divide to form two dyad cells each. The ne division was observed in two or three cases only, and it was found to be simultaneo in both the dyad cells. Although several tetrads are present, a freshly formed row megaspores can be easily recognized, as it retains the spindle-shaped form of the mothe cell from which it is derived.



Text-fig. 32. Diagrams showing development of megaspores and embryo sac. The insets *a–e* represen entire flowers at half the natural size. A. L.S. ovary showing archesporial tissue. B. L.S. ovar showing megaspore mother cells. C. L.S. ovary showing megaspore tetrads and megaspore mothe cells. Note gradual closing up of ovary cavity. D. Older stage showing gliding growth of th megaspore cells and their derivatives. Note degeneration of cells separating the young embry sacs. E_1, E_2, E_3. Basal, middle and upper part of gynoecium in L.S. Note the egg apparatuse in the style and antipodal cells pressed against the collenchymatous pad (*col*) just above the bas of ovary.

Sometimes more than four cells—as many as eight—were seen in a single row (Text fig. 35 and Pl. 23, fig. 2). Such a condition may be due to two factors: either there is further division of some or all of the megaspores, or the additional cells originated from second megaspore mother cell situated in the same row as the first. I consider the latte to be the more probable explanation.

Treub (1881), in *Macrosolen cochinchinesis* and Rauch (1936), in *Scurrula atropurpure* and *Dendrophthoe pentandra*, report a row of three cells of which the uppermost function to give rise to the embryo sac. They do not explain, however, whether the functional cel s a dyad cell or a megaspore. Schaeppi & Steindl (1942) report that in *Macrosolen ochinchinesis* there is a row of three cells of which one is binucleate.[1]

My observations on *Dendrophthoe falcata* show that all four megaspores of a tetrad, xcepting the one lying towards the upper part of the ovary, have the power of further rowth. Text-fig. 36 shows a binucleate embryo sac formed from the second cell of the etrad. In another instance the second and the fourth cells from above had enlarged while he other two had degenerated. Sometimes three two-nucleate embryo sacs were seen in single row suggesting that they had developed from three megaspores of the same etrad.

Since there is a massive sporogenous tissue, a large number of megaspores is formed and heir elongation is very rapid. This tissue of gliding and closely interlocking cells resembles he hymenial layer of a fungus. Treub and Rauch have also called attention to this point.

During their rapid growth a large number of the megaspores are crushed and appear as lark streaks in slides stained with iron-alum haematoxylin. A study of the later stages of levelopment, therefore, presents many difficulties. Many of the slides that had been liscarded by me in a preliminary study on account of widespread degeneration revealed everal stages of embryo sac development. By this time the epidermal layer lining he cavity of the ovary is almost crushed out of recognition (Pl. **23**, fig. 3), and the ovary avity has been obliterated. The two-nucleate embryo sacs (Text-fig. 36 and Pl. **23**, ig. 3) are surrounded by a large number of degenerating or degenerated cells, among vhich it is not uncommon to find a few other embryo sacs which became arrested in their levelopment.

In slightly older flowers we see eight-nucleate embryo sacs with their proximal ends n the ovary and the distal ends in the base of the style. Text-fig. 37 shows the levels at vhich different parts of the embryo sacs are found. In one of the embryo sacs (lying etween *b* and *c*) I saw the egg apparatus, the upper polar nucleus, and another nucleus, robably the lower polar, lying at some distance below the former (Text-fig. 38). The ntipodal ends of mature embryo sacs (Text-figs. 39 and Pl. **23**, fig. 4) reach as far down s the collenchymatous pad which is in the lower part of the ovary.

Longitudinal sections of the style show smaller embryo sacs in its basal part and larger nes in the upper part. This indicates that the sacs are already organized while they are et in the basal part of the style, but they continue to elongate and grow upward into the tyle. The cells that happen to lie in their path are dissolved and the tips of the embryo sacs o on winding upwards till they have reached a height of 22–28 mm. from the pad of ollenchyma. In one case the apical end of an embryo sac was found to be at a distance f 38 mm. (measured in a straight line) from the collenchymatous pad. As the style is rom 45 to 50 mm. long, it is only the distal 15 mm. or so which remains uninvaded by mbryo sacs (Text-fig. 37, above level *d*). This elongation of the embryo sacs, both towards he top and the bottom, is a very remarkable feature, which is nowhere so pronounced s in the Loranthoideae.

The upper end of the embryo sac occupies nearly the whole width of the stylar canal. t possesses a prominent egg (Text-figs. 40, 41) and two synergids which (Text-fig. 38) re hooked in younger stages and also show a filiform apparatus. The upper polar nucleus ies close to the egg (Text-figs. 40, 41).

Just below the egg apparatus the embryo sac suddenly becomes very narrow. In ongitudinal sections it is distinguishable from the surrounding cells of the style by its lenser cytoplasm and tortuous course. As the number of such meandering embryo sacs s fairly large (7–10), the stylar tissue presents a rather complicated appearance.

Proceeding downwards, the embryo sacs follow a still more tortuous path in the ovary, nd their basal ends containing the antipodals become embedded in the degenerated issue in its lower part. The antipodals press against the pad of collenchyma. Text-fig. 39

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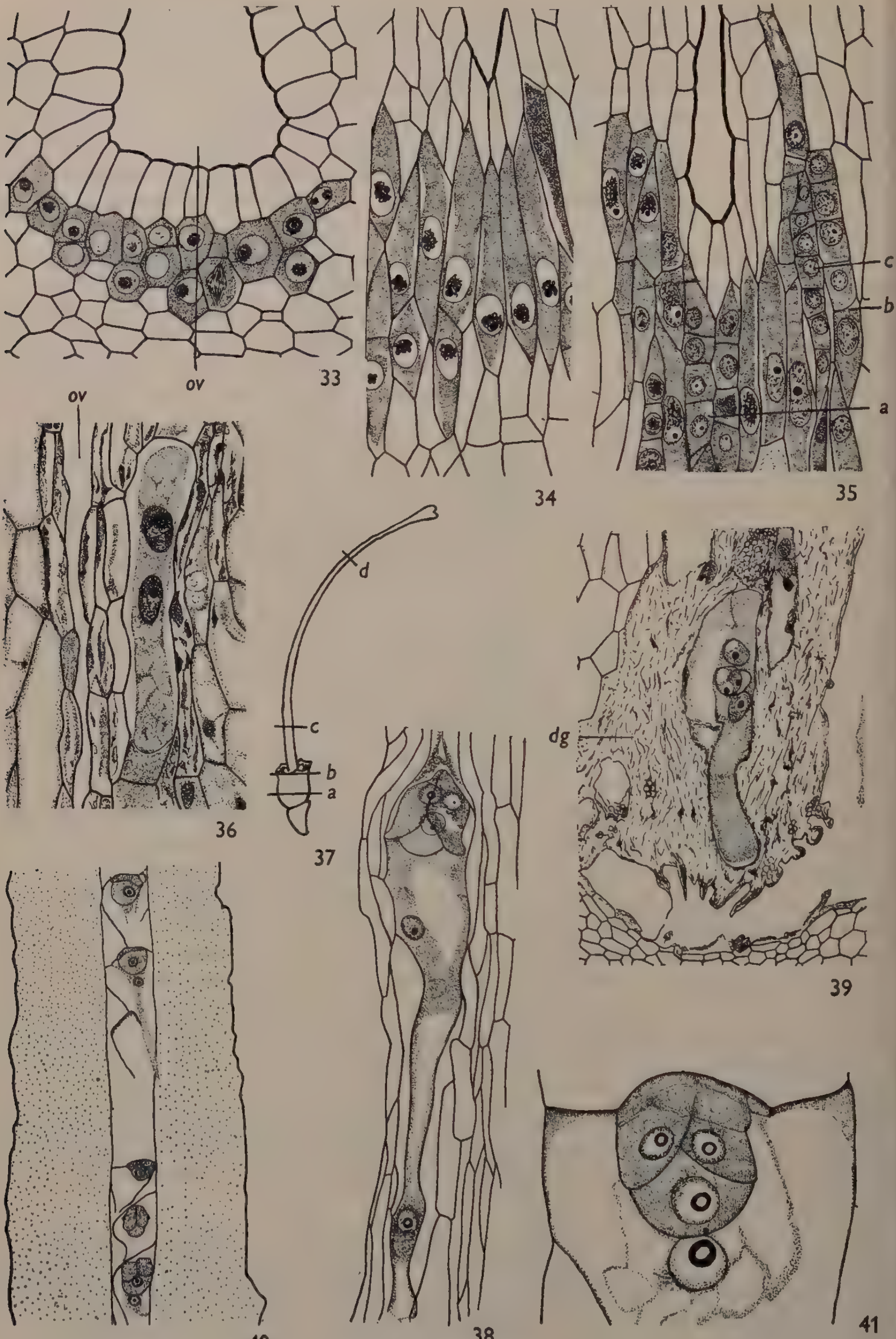
[1] Recently I had an opportunity of examining some slides of this plant prepared by Prof. P. aheshwari, showing undoubted linear tetrads of megaspores.



Text-figs. 33–41. For legends see p. 463.

hows four nuclei belonging to the lower end of the embryo sac. One of these must be the ower polar nucleus and the other three the antipodal nuclei. The antipodals organize hemselves into cells, but owing to their early degeneration they are not easy to find. he embryo sacs are undoubtedly eight-nucleate, as in other members of the Loranthoideae, ut I must confess that I could not succeed in tracing any individual embryo sac from one nd to the other.

I stated on page 459 that some of the mother cells become arrested in their development. hey may resume their growth later but rarely proceed beyond the two-nucleate stage.

ENDOSPERM

could not observe any fusion of the polar nuclei, but I presume that it takes place in the ower part of the embryo sac as endosperm formation begins at this end. Text-fig. 42 hows a series of diagrams representing the development of the endosperm and embryo. he earliest stage of the endosperm observed by me showed four cells (Text-fig. 42 A_1), nd it seems reasonable to suppose that it is cellular from the very beginning as in all ther members of the family so far studied.

The endosperm cells enlarge so quickly that their cytoplasm is not able to keep pace ith their growth, and it forms only a thin peripheral layer containing the nucleus Pl. **23**, figs. 5, 6). Cell formation progresses towards the top of the ovary, in which region he endosperm cells are extremely elongated (Text-fig. 42 B). A cross-section at this level hows only four or five endosperm cells in each embryo sac (Text-figs. 42 C, D, 43 and Pl. **23**, igs. 5, 6). The pro-embryo passes down between these cells into the lower part of the vary where the cells of the endosperm are broader. Meanwhile, the degenerating cells *rm*) separating the individual embryo sacs (Text-fig. 42 B, C) are slowly consumed so that he sacs lie in contact with one another (Pl. **23**, fig. 6).

A rapid growth of the endosperm now ensues by repeated divisions of its cells, which ecome progressively smaller in size and more densely cytoplasmic. Due to the disappearance of the separating walls the endosperms of individual embryo sacs can no longer e distinguished, all fusing to form a composite mass containing a number of embryos Text-figs. 42 B, D, 44 and Pl. **23**, fig. 6).

Further growth of the endosperm takes place at first in an upward direction after which ts base forms an annular bulge around the collenchyma (Text-fig. 45, *col*). Later one ide of the bulge begins to grow down faster pushing the collenchymatous pad laterally Text-fig. 46, *col*). A similar condition has been figured by Rauch in *Scurrula atropurpurea* and *Dendrophthoe pentandra* and Schaeppi & Steindl (1942) in *Taxillus tomentosus*. he parenchymatous cells situated below the pad of collenchyma now present a somewhat shrivelled appearance and develop numerous intercellular spaces. They are soon nvaded and consumed by the advancing endosperm.

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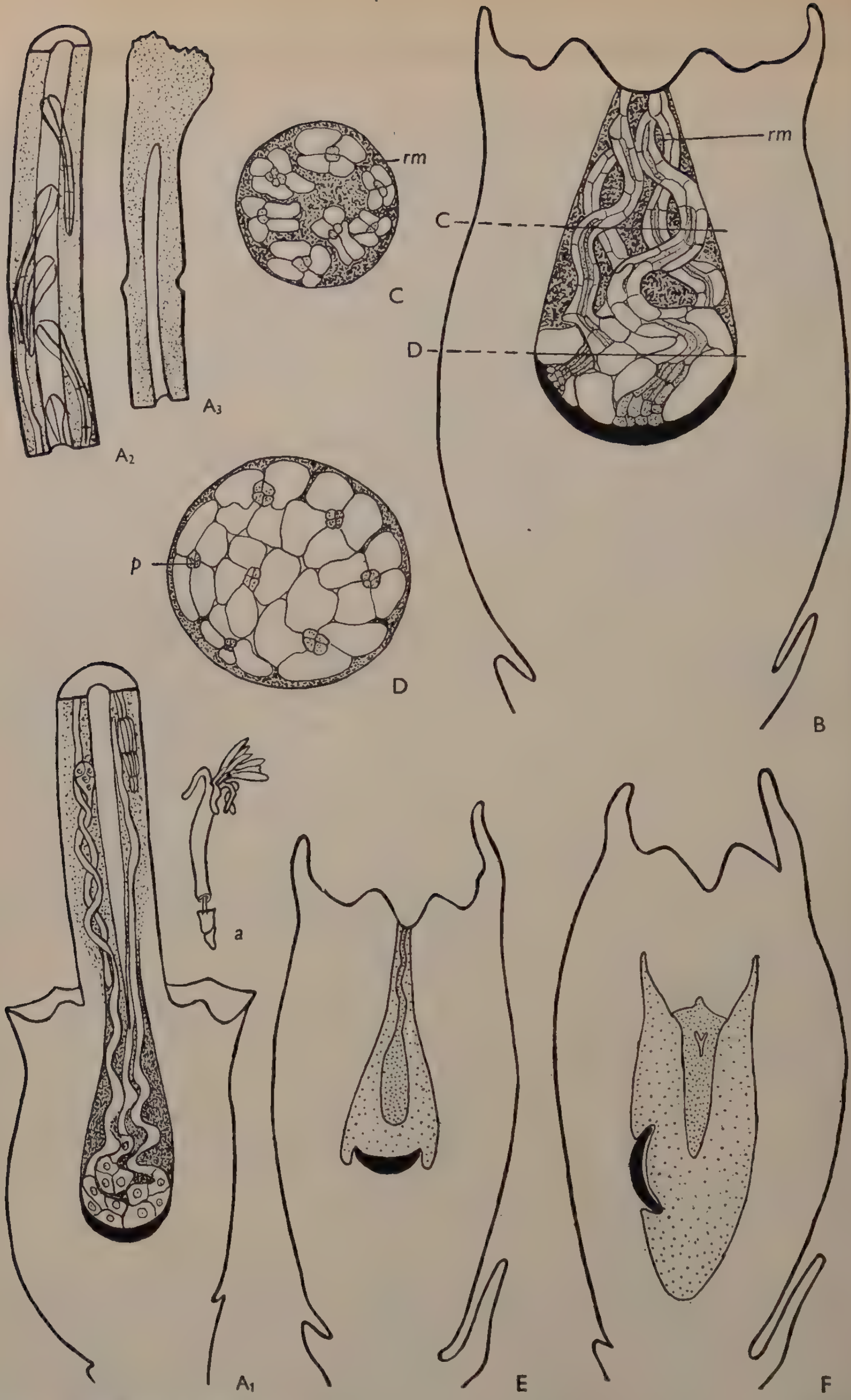
ext-figs. 33–41. Megasporogenesis and female gametophyte. Text-fig. 33. L.S. ovary showing the hypodermal archesporium (*ov* = ovarian cavity). × 475. Text-fig. 34. L.S. ovary with megaspore mother cells in synizesis. × 475. Text-fig. 35. L.S. ovary showing rows of megaspores and some undivided mother cells (note rows of 4, 5 and 7 megaspores at *a*, *b* and *c* respectively). × 475. Text-fig. 36. Part of ovary showing a two-nucleate embryo sac; note gradual obliteration of ovarian cavity (*ov*). × 475. Text-fig. 37. Pistil from open flower. When the embryo sacs are mature, their antipodal ends lie between the levels *a* and *b* and the egg apparatus ends at first lie between the levels *b* and *c* but later grow up to the level *d*. × Natural size. Text-fig. 38. Embryo sac as observed in wall of style, approximately between the levels *b* and *c* of Text-fig. 37. × 195. Text-fig. 39. L.S. ovary showing the obliquely cut end of an embryo sac with three antipodal nuclei and the lower polar nucleus (*dg* = degenerated cells lying between different embryo sacs). × 475. Text-fig. 40. L.S. style showing distal ends of embryo sacs in the stylar canal. × 87. Text-fig. 41. Upper end of mature embryo sac showing the egg apparatus and the upper polar nucleus. × 475.



Text-fig. 42. Diagrams showing development of endosperm and embryo. A$_1$, A$_2$, A$_3$. Lower middl and upper portions of gynaeceum showing position of pro-embryos (the inset *a* represents a flowe of this stage at approximately half the actual size. B. L.S. young fruit showing several pro-embryos; note composite endosperm at base, formed by a fusion of the lower ends of several embryo sacs. C. T.S. of same at level C showing seven embryo sacs with endosperm and pro-embryo. D. T.S. of same at lower level D showing a stage in the fusion of the endosperms of all the embryo sacs; note pro-embryos *p*. E. L.S. older fruit showing ring-like growth of endosperm around collenchymatous pad. F. L.S. nearly mature fruit; the pad of collenchyma has been pushed to one side and the radicle end of the embryo projects above the endosperm.

EMBRYO

The first few divisions of the zygote could not be observed in my material. Text-fig. 47 and Pl. **23**, fig. 7, show a long, narrow pro-embryo composed of a double row of cells. This stage is found in flowers whose perianth is about to fall off. Griffith (1844) found the first division of the egg of *Dendropthoe falcata*, *Scurrula parasitica* and *Macrosolen cochinchinensis* to be longitudinal, and Treub (1881) confirmed it in *Macrosolen cochinchinensis* and *Dendrophthoe pentandra*. Rauch (1936) did not see the earlier divisions of the egg in *Scurrula atropurpurea*, but from the appearance of the pro-embryos he concludes that the first division of the egg is longitudinal, and is followed by a series of transverse divisions. Schaeppi & Steindl (1942) also report the same in *Taxillus tomentosus*.

From the regularly biseriate nature of the pro-embryo of *Dendrophthoe falcata* (Text-fig. 47 and Pl. **23**, fig. 7), and from the position of its cells it may be concluded that the first division is longitudinal just as in the other members of the Loranthoideae cited above.

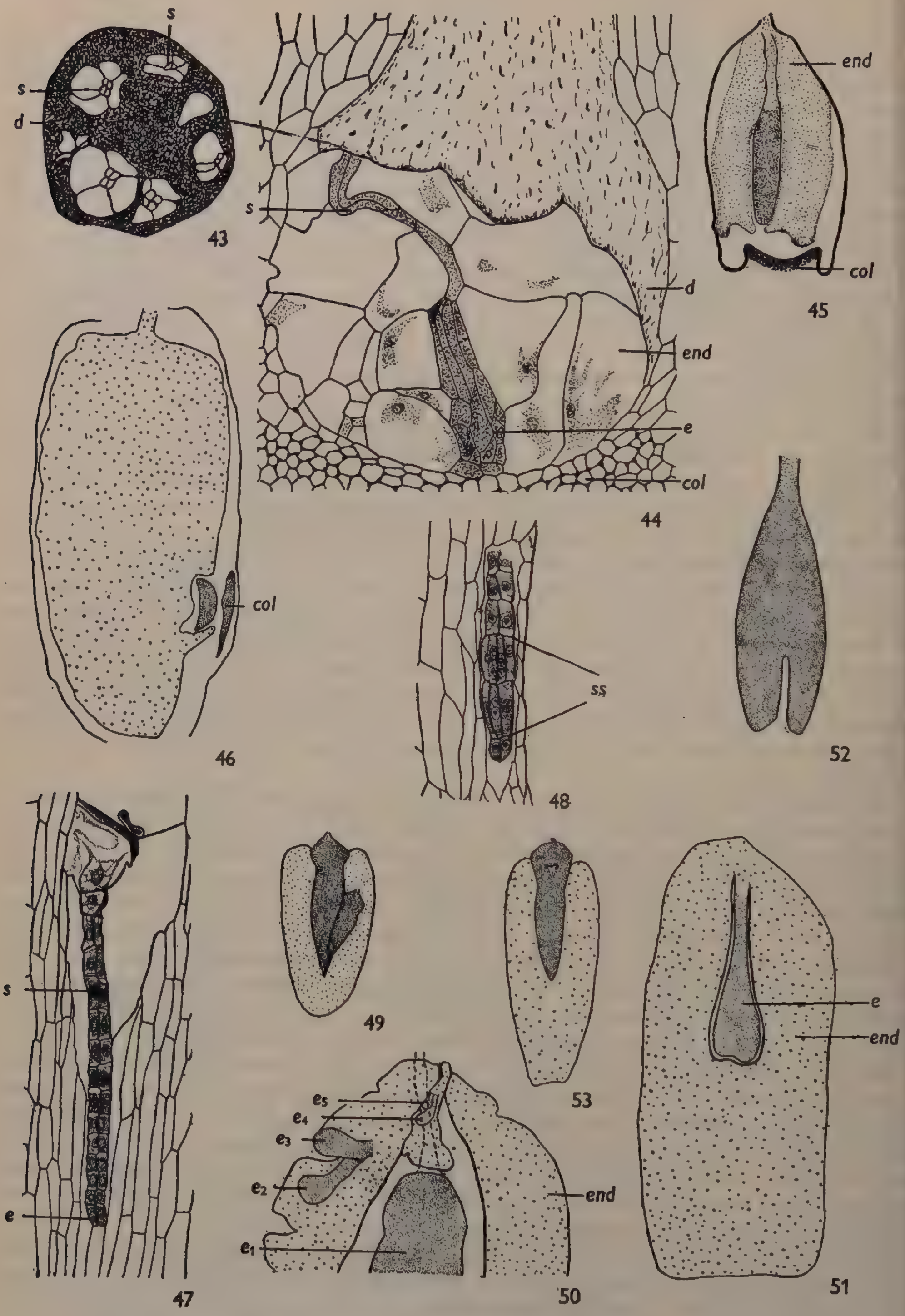
The embryo proper develops from the two terminal cells of the pro-embryo. By an elongation of the remaining cells which form the suspensor it is carried down into the stylar canal for some distance, after which it enters the wall of the style. At this stage, the suspensor cells lying just behind the terminal cells undergo another vertical division (Text-fig. 48) so that a cross-section of this part shows a group of four cells. When the pro-embryo enters the base of the ovary, the cells of the suspensor become very long and narrow. The embryos themselves lie in the composite endosperm formed by the amalgamation of all the embryo sacs (Text-fig. 42 C, D and Pl. **23**, figs. 5, 6).

Generally only one embryo grows down to the pad of collenchyma (Text-fig. 44) and continues further development. The rest usually degenerate and are absorbed in the tissue of the endosperm. In one ovary I found two nearly mature embryos (Text-fig. 49). In another several smaller embryos (Text-fig. 50) were found in the upper part of the endosperm, together with one embryo in a more advanced stage of development. Weir (1914) reports polyembryony to be quite common in *Razoumofskya*. Since only one embryo arises from each embryo sac in the Loranthaceae these must be considered to be cases of false polyembryony.

Those cells of the embryo, which touch the pad of collenchyma, stain more densely than those belonging to its upper part. The former divide actively (Text-figs. 42B, 45) accompanied by repeated divisions of the endosperm cells. At the same time there are some adjustments in the spatial relations between the endosperm and embryo so that the latter comes to occupy a more median position in the endosperm a part of which extends between the terminal part of the embryo and the pad of collenchyma (Text-figs. 42B, 51). The embryo is pulled up by the coiling of the cells of the suspensor to bring about this change of position of the embryo. Meanwhile, the embryo assumes a club-shaped appearance and the two cotyledons begin to differentiate and grow at the tip (Text-fig. 52). In the mature stage, however, they fuse to form a single conical organ. The fact that the monocotyledonous nature of the embryo of *Dendrophthoe falcata* is not due to a suppression of one of the cotyledons but is the result of their fusion is also clear from their vascular supply as seen in cross-sections of the embryo (Text-figs. 54–57). Text-fig. 54 shows four vascular bundles at the place of origin of each cotyledon. Lower down these divide to form several strands (Text-figs. 55, 56), but near the tip the number is again reduced as the marginal bundles become arrested in their growth. The central vascular strands alone persist to the apex of the fused cotyledons (Text-fig. 57).

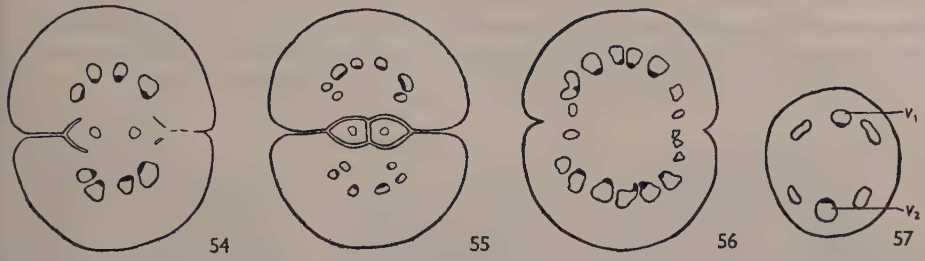
In a cross-section of one embryo I noticed three cotyledons which were free at the base (Text-fig. 58A, B) but fused towards the apex (Text-fig. 58C). The fused part showed the vascular supply of all the three cotyledons.

The mature embryo is green and varies from 8 to 10 mm. in length. Text-fig. 53 and Pl. **23**, fig. 8, show its appearance in a longitudinal section. It possesses a cushion-like radicle end with an equatorial ring of small papillae whose morphological nature is

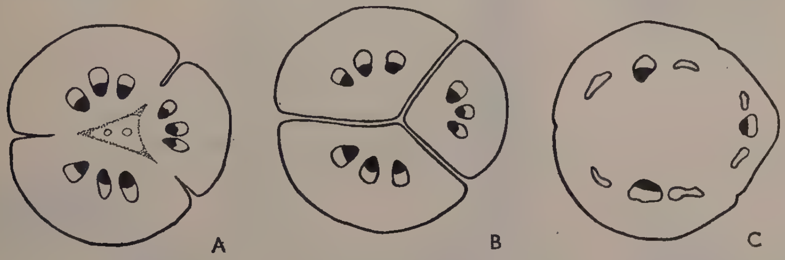


Text-figs. 43–53. For legends see p. 467.

unknown. Just below the radicle end the embryo is more or less cylindrical for approximately two-thirds of its length. The remaining one-third gradually tapers down to form a pointed tip.



Text-figs. 54–57. T.S. of an embryo. Text-fig. 54. T.S. mature embryo at the level of origin of the cotyledons showing four vascular strands in each cotyledon. The two traces in the centre belong to the first pair of leaves. × 31. Text-fig. 55. Same at a lower level, showing free parts of the cotyledons surrounding the first pair of leaves. × 31. Text-fig. 56. T.S. further down the cotyledons. × 31. Text-fig. 57. T.S. towards cotyledonary apex. Only two vascular bundles marked v_1 and v_2 persist beyond this level. × 31.



Text-fig. 58. Transverse sections of an abnormal embryo having three cotyledons: A, at level of origin of cotyledons; B, at lower level showing free parts of cotyledons; C, further down, showing fused cotyledons. × 33.

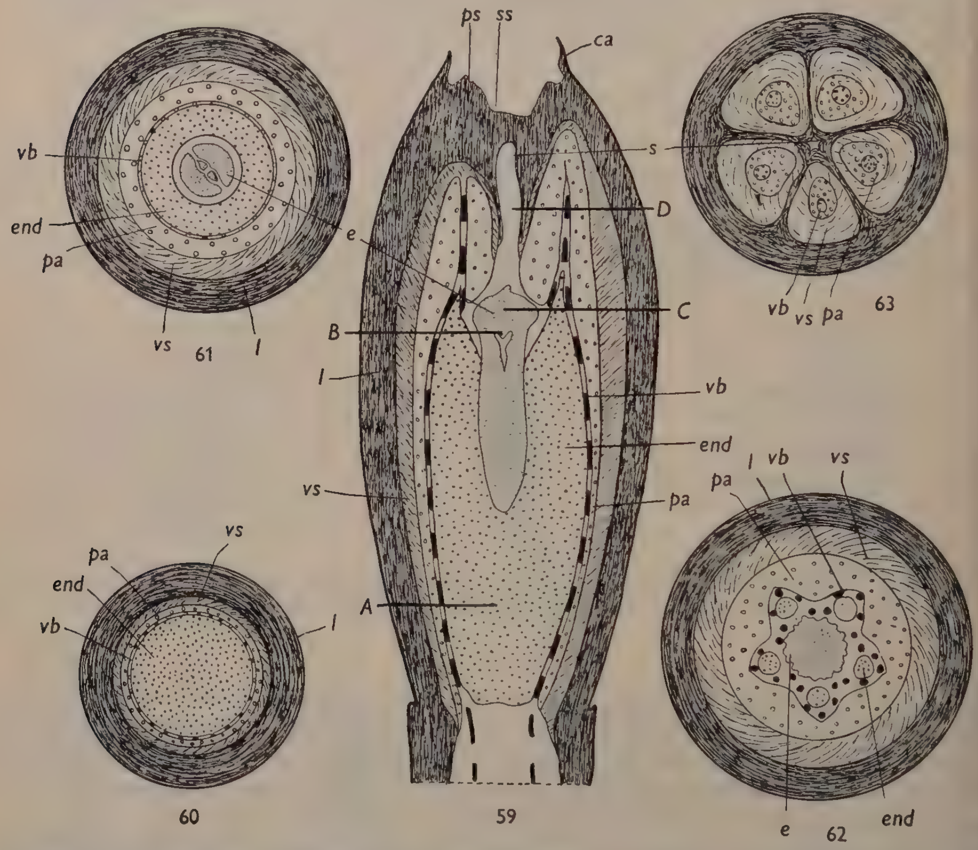
Fruit

The fruit is characterized by the following features: (*a*) absence of a testa around the seed, (*b*) the peculiar form of the endosperm, and (*c*) the complex nature of the fruit wall which is composed of four well-defined zones. The structure is specially complicated in the distal part of the fruit because of the formation of five apical processes from the endosperm, each of which is itself enveloped by the four zones of the fruit wall.

In order to obtain a clear picture of the anatomy of the fruit it is necessary to compare the longitudinal sections (Pl. **23**, figs. 8, 9) with serial cross-sections (Pl. **23**, figs. 10–17). For further elucidation a reference may be made to Text-figs. 59–63.

Text-figs. 43–53. Development of embryo and endosperm. (*col* = collenchyma pad; *d* = degenerated cells; *e* = embryo; *end* = endosperm, *s* = suspensor cells). × 20. Text-fig. 43. T.S. portion of ovary showing several embryo sacs which are separated from one another by large masses of degenerated cells (*d*). × 186. Text-fig. 44. L.S. part of ovary showing embryo, mass of endosperm cells and the degenerated cells. × 195. Text-fig. 45. L.S. composite endosperm with a single embryo. The shrinkage of the endosperm is due to poor fixation. Text-fig. 46. The endosperm has pushed the collenchymatous pad to one side and has grown to the base of the ovary. × 67. Text-fig. 47. Oblique longitudinal section of the style showing a biseriate pro-embryo. × 195. Fig. 48. L.S. wall of style showing a part of the pro-embryo. At *ss* the suspensor cells have undergone another vertical division. × 195. Text-fig. 49. L.S. endosperm with two nearly mature embryos. × 20. Text-fig. 50. Same, with five embryos (reconstructed from eight sections). × 67. Text-fig. 51. L.S. endosperm containing embryo at the time of initiation of the cotyledons. × 20. Text-fig. 52. L.S. embryo showing the two cotyledons. × 67. Text-fig. 53. L.S. nearly mature embryo embedded in the endosperm. × 10.

In a mature fruit the endosperm reaches down to its base. All the cells of the ovary, internal to its vascular supply, are consumed by it leaving only a thin band of crushed parenchyma. The shape of the mature endosperm may be compared to a flower vase, with very massive walls and an even more massive basal part, which is narrow below, gradually widens towards the middle and narrows again into a neck surmounted by the five sharply conical outgrowths (Text-fig. 64). The embryo fits into the cavity of the endosperm, only its upper end projecting between the five processes of the endosperm.



Text-figs. 59–63. Diagrams of sections of fruit. (*ca* = calyculus; *e* = embryo; *end* = endosperm; *pa* = zone of parenchyma; *ps* = perianth scar; *l* = leathery coat of the fruit wall; *s* = space through which the embryo sacs pass into the ovary; *ss* = scar of style; *vb* = vascular zone; *vs* = viscid layer.) Text-fig. 59. L.S. fruit. Text-figs. 60–63. T.S. of same at the levels A, B, C and D respectively.

In a ripening fruit the cells of the endosperm show small vacuoles and their nuclei are dark and deformed. The outer cells, which are adjacent to the ovary wall and the inner which lie in contact with the embryo, are of a smaller size than the rest. Mayr (1926) describes the presence of albumen crystals in the endosperm of *Hyphear europaeum* (Jacq.) Dans.

The fruit wall comprises the following layers (from within outwards):

(i) A vascular zone (Text-fig. 59, *vb*), which envelops the endosperm (*end*) like a tube. This consists of elongated and crushed parenchyma cells with the vascular bundles running longitudinally. (The distribution of the bundles is shown in Text-figs. 60 and 63.)

(ii) A parenchymatous zone composed of rather large cells (*pa*) with vacuolate cytoplasm. This zone is considerably thicker in the distal one-third of the fruit.

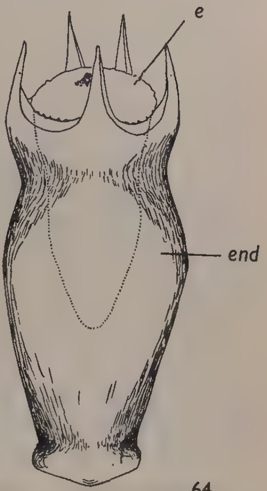
(iii) A viscid zone formed of much elongated thin-walled cells (*vs*) which are diagonally oriented as seen in a longitudinal section of the fruit (Pl. **23**, fig. 8). In cross-sections these cells show an obliquely radial alinement. A smear preparation showed them to be much longer than the sections would indicate, suggesting that they are spirally coiled somewhat like the bristles of a twisted wire brush. This deceptive appearance may be compared to that of the single layer of obliquely oriented starch cells in the glossy petals of many species of *Ranunculus* (Parkin, 1928, 1931; Singh, 1936).

(iv) A thick leathery coat (*l*) which forms the outer wall of the fruit. This is for the most part composed of small parenchymatous cells mixed with scattered patches of stone cells, followed by two layers of a thin-walled hypodermis and the epidermis.

A study of successive transverse sections of the fruit gives the relative sizes and arrangement of the tissues at various levels. Stone cells are abundant in the basal part of the fruit (Pl. **23**, fig. 10). At this level the vascular strands passing into the fruit do not show any regular arrangement. Higher up they are seen only in the innermost layers of the fruit wall (Text-figs. 59–61 and Pl. **23**, figs. 10–12).

Close to the radicle end of the embryo the arrangement of the various tissues begins to show some changes. At this level (Pl. **23**, fig. 8, *V*) the endosperm is present only in five patches (*end*) which are the transversely cut ends of its conical prongs (Text-fig. 62 and Pl. **23**, fig. 13). Each of these patches is surrounded by the vascular zone (*vs*).

At level *W* (Pl. **23**, fig. 8) the endosperm has disappeared and the wavy vascular zone is seen to be divided into five patches (Pl. **23**, fig. 14) which are surrounded by a thick layer of the large parenchymatous cells of the second zone. Slightly higher up (Pl. **23**, fig. 15) this layer of parenchyma also becomes divided into five more or less circular patches which really form five finger-like processes separated from one another by the wedge-shaped ingrowths of the viscid layer (*vs*). The central part of the fruit (Pl. **23**, figs. 8, 16) shows the crushed and degenerated remains of the embryo sacs. The outermost part of the fruit wall, i.e. the leathery zone, also shows similar but narrower wedges projecting into the viscid layer. They appear as five radial septa which meet in the centre of the fruit so as to divide the viscid layer with its enclosed tissue into five lobes (Text-fig. 63, Pl. **23**, fig. 16). Towards the distal end of the fruit (Pl. **23**, fig. 17) the septa become broader while the lobes become more and more reduced in size until they terminate just below the calyculus.



Text-fig. 64. Perspective view of mature endosperm (*end*) and embryo (*e*). Note the five prongs formed by the apical part of the endosperm. ×c. 20.

Conclusion

The outstanding features in the embryology of *Dendrophthoe falcata* are as follows:

(i) The absence of a well-defined nucellus or integument;
(ii) the penetration of the embryo sac into the style;
(iii) the abscission of the style in two stages, the upper part of the style (5–7 mm.) falling off first and then the lower;
(iv) the composite endosperm formed by a fusion of the endosperms belonging to several embryo sacs;
(v) viscid fruit wall surrounding the embryo.

Owing to the absence of any well-defined nucellus the place of origin of the female gametophyte is a morphological puzzle. Griffith (1844) reported a free central placenta in this plant but my observations, which are in agreement with those of Rauch (1936) on

Scurrula atropurpurea and *Dendrophthoe pentandra*, show that there is neither a placenta nor any ovules in the usual sense.

The development of the embryo sac is of the *Polygonum* type, which appears to be a constant feature in the subfamily Loranthoideae. After the two-nucleate stage, the sac shows considerable upward elongation. Subsequently, the lower end also elongates reaching down to the collenchymatous pad. Even after the formation of the egg-apparatus the upper end continues to advance through the tissues of the style and finally comes to lie in the stylar canal.

The height to which embryo sacs grow in different genera is very variable as shown by Schaeppi & Steindl (1942). In *Dendrophthoe falcata* I find that the embryo sacs stop short of the stigma by about 15 mm. only, the total length of the style being 45 mm. This prolongation of the embryo sacs into the style creates some doubt as to its morphological nature.[1] Approximately 5–7 mm. below the stigma, i.e. slightly above the point reached by the sacs, the styles are often bent rather abruptly. This distal portion of the style, which frequently also shows a difference in colour as compared to the lower part, falls away earlier suggesting that the lower part may really belong to the ovary and that only the part above the bend represents the true style. It would be interesting to check this hypothesis with the help of comparative studies on other members of the Loranthoideae.

The upper polar nucleus travels a long distance down into the part of the embryo sac which lies in the ovary, and it is here that the development of the endosperm takes place. As in *Scurrula atropurpurea* and *Dendrophthoe pentandra* (Rauch, 1936), the endosperms of the different embryo sacs fuse to form a composite mass.

The extraordinary development of the suspensor which brings the pro-embryo down into the tissue of the endosperm is very remarkable, especially as this elongation has to take place rapidly before the shedding of the style-like organ, or else the embryo would perish along with the style.

The chief peculiarity of the fruit of *D. falcata*, as of other plants of this family, is the presence of a viscid layer whose cells, like the spirally arranged bristles of a wire brush such as is commonly used for cleaning the barrel of a rifle, show a torsion which under the turgid conditions of the cells may be instrumental in facilitating the ejection of the seed.

In conclusion it may be said that the organization of the embryo sac, endosperm and embryo of the Loranthoideae is unique in many ways. The morphology of the structure in which the archesporial cells originate, as well as of the so-called style in which the egg apparatus are ultimately lodged, is a question which can be answered only after further research.

SUMMARY

1. The flower is pentamerous. There is a five-toothed calyculus and a perianth tube, which opens at the tip into five reflexed lobes and bears five epiphyllous stamens. The ovary is inferior.
2. The floral organs arise in acropetal succession.
3. The vascular anatomy of the flower is based on a pentamerous plan. The perianth tube receives five vascular traces each of which divides to form three to five bundles. The stamens receive one trace each, and five traces enter the style. In the stigmatic region they further subdivide into seven to ten bundles.
4. The anther wall is formed of four layers besides the epidermis. These are the endothecium, two middle layers, and the tapetum. The tapetum remains uninucleate.
5. The microspore mother cells divide simultaneously to form microspore tetrads of tetrahedral and decussate types.

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[1] It is true that there are a few records of ovules lying in the open stylar canal, and of some naked nucelli inside the ovary (see Capoor, 1937), but these are in the nature of abnormalities and cannot be compared with the condition in *Dendrophthoe*.

6. The pollen grains are shed at the two-celled stage. The division of the generative cell, which takes place in the pollen tube, shows clear spindle fibres accompanied by cell-plate formation.

7. The archesporial tissue differentiates in the hypodermal layer at the bottom of the ovary cavity.

8. The megaspore mother cells give rise to linear tetrads of megaspores. All the megaspores except those lying towards the upper end are capable of further development. As a result of the enlargement and gliding growth of the megaspores the ovary cavity is soon obliterated.

9. The embryo sac is eight-nucleate. The upper ends of the embryo sacs grow into the wall of the style, while the lower ends grow downwards so as to reach the pad of collenchymatous cells situated in the basal part of the ovary. A well-developed embryo sac is approximately .22–28 mm. in length.

10. The first division of the egg is longitudinal. Owing to an extreme elongation of the suspensor the pro-embryos are pushed down into the ovary. Only one embryo reaches maturity.

11. The endosperm is cellular and is initiated in the lower part of the embryo sac. Due to a dissolution of the separating walls of the embryo sacs all the endosperms fuse to form a composite mass.

12. There is no testa. The wall of the fruit comprises four layers of tissues. Of these the second (counting from outside), or the viscid layer, is very characteristic and is responsible for the ejection of the seed and its adhesion.

Acknowledgements

I owe a debt of gratitude to Prof. P. Maheshwari, who suggested the problem and gave me his valuable advice and guidance. I also wish to express my indebtedness to the late Prof. B. Sahni for his generous guidance during the progress of this work. I desire to thank the government of the United Provinces for a research grant for studies on the morphology of the Loranthaceae, and to Principal R. K. Singh, Balwant Rajput College, Agra, for facilities and encouragement.

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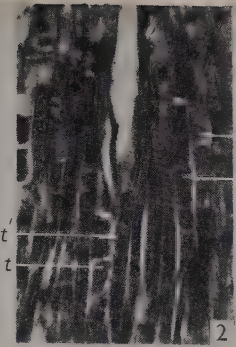

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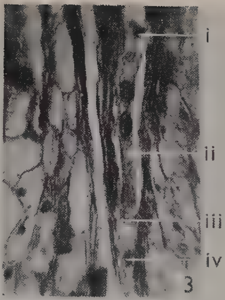

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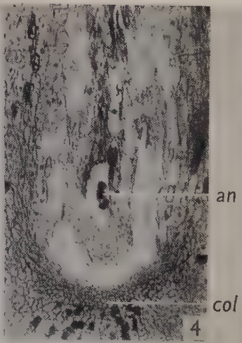

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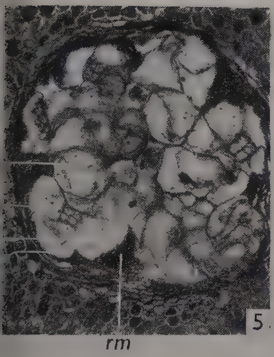

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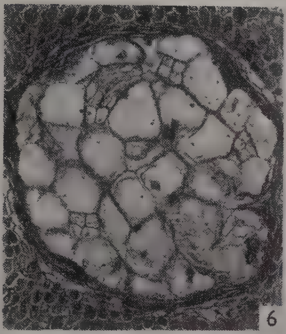
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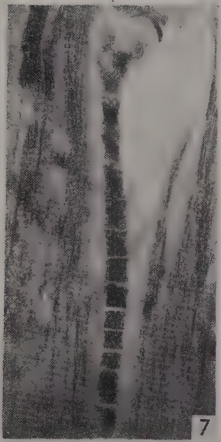
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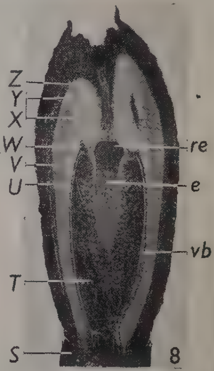

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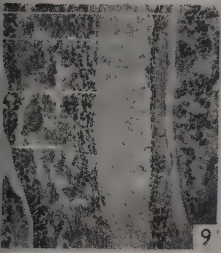
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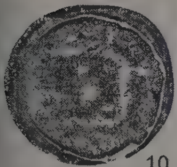
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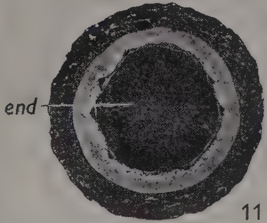

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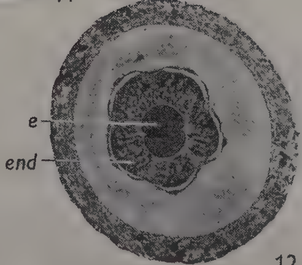

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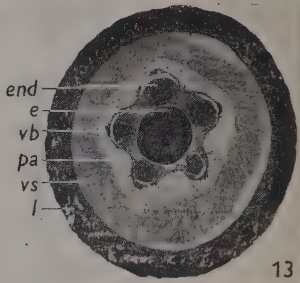

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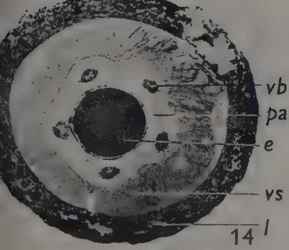

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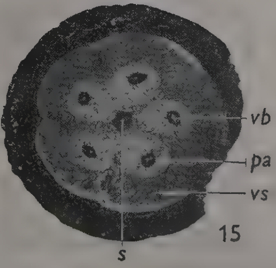

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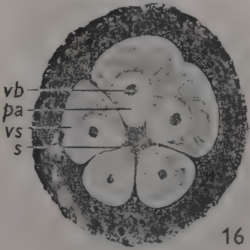

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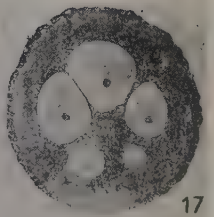
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Dendrophthoe falcata

EXPLANATION OF PLATE 23

Figs. 1–17. Photomicrographs showing development of *e.s.*, *e*, *end* and structure of fruit. (*a–d* = endosperm cells; *an* = antipodal nuclei; *col* = pad of collenchyma; *e* = embryo; *end* = endosperm; *e.s.* = embryo sac; *l* = outer wall of fruit; *mmc* = megaspore mother cell; *pa* = zone of parenchyma; *re* = radicle end of embryo; *rm* = remnants of cells separating different embryo sacs; *s* = path of embryo sacs into the ovary; *t* = linear tetrad of megaspores; *t′* = row of five megaspores, the central cell degenerating; *t″* and *t‴* = seven and eight megaspores in a row; *vb* = vascular zone; *vs* = viscid layer. Figs. 1, 2. L.S. adjacent part of ovary showing megaspore mother cells and megaspore tetrads. × 694. Fig. 3. L.S. part of ovary showing a binucleate *e.s.* formed by the second cell of the *t* (i–iv). × 475. Fig. 4. L.S. ovary showing the antipodal end of an *e.s.* containing four nuclei one of which is the lower polar nucleus. × 114. Fig. 5. T.S. part of ovary with T.S. of *e.s.* each showing four or five *end* cells. × 186. Fig. 6. T.S. ovary at a lower level showing fusion of different *e.s.* to form a composite *end.* × 186. Fig. 7. Oblique longitudinal section of the style showing an elongated biseriate pro-embryo. × 350. Fig. 8. Radial longitudinal section of fruit. × 6. Fig. 9. L.S. wall of the fruit at a higher magnification. × 22. Figs. 10–17. Cross-sections of the fruit the levels *S–Z* shown in fig. 8. × 11.

Embryological studies on Spiranthes australis Lindl.[1]

By P. Maheshwari and S. Narayanaswami, University of Delhi, India.

(With 72 Text-figures)

(Communicated by C. R. Metcalfe, M.A., Ph.D., F.L.S.)

[Read 10 May 1951]

Introduction

A terrestrial orchid, *Spiranthes australis* Lindl., was collected by us a few years ago from a marshy place near Tejgaon, about four miles from the town of Dacca in East Bengal. Some plants from the original locality were also grown in the Dacca University Botanical Gardens so that a ready supply of material was available.[2] In June 1949, one of us (P.M.) collected further material from Khatmandu, Nepal, during a short visit to that place as a member of a scientific and cultural mission sponsored by the government of India.

The plant is 6–24 in. high with four to five leaves clustered around its base, and numerous small flowers developing in acropetalous succession on long spirally twisted spikes. Formalin-acetic alcohol and Nawaschin's fluid were used for fixation, and the material was imbedded in paraffin in the usual way. Sections were cut 5–8 μ thick, and stained in iron haematoxylin and safranin-fast green.

Previous work

Several papers have appeared on the embryology of orchids (see Schnarf, 1931). Among recent studies may be mentioned those of Afzelius (1928, 1932) on *Nigritella*, Hagerup (1944, 1945, 1947) on *Orchis*, *Epipactis* and *Cephalanthera*, and Swamy (1948, 1949*a*, *b*) on a variety of other genera. The tribe Spirantheae includes sixteen genera, of which only five have been studied embryologically: *Neottia*, *Zeuxine*, *Listera*, *Goodyera* and *Spiranthes*. Concerning the last-named genus, Leavitt (1901) reported the general occurrence of polyembryonate seeds and suspensorless embryos in *S. cernua*. Pace (1914), working on *Gyrostachys* (= *Spiranthes*) *gracilis* and *G. cernua*, stated that megasporogenesis and embryo-sac development in these plants could take place in any of the following ways: normal, *Allium* or *Adoxa* type.[3] She further observed that the embryo sacs were five-nucleate. In *Spiranthes australis*, according to Baranow (1915), the embryo sac is of the *Polygonum* type. Swamy's (1948) recent studies on *S. cernua* have revealed the existence of three distinct races of this species in the U.S.A., viz. the sexual, the agamospermic and the 'intermediate'. The sexual race showed normal fertilization and the production of a single embryo in each seed. In the agamospermic race the pollen as well as the embryo sac were functionless, and two to six adventive embryos were formed in each seed by a proliferation of the cells of the integument. In the 'intermediate' forms part of the ovules of an ovary followed the first course and the rest the second course.

The flower

The perianth comprises two trimerous whorls consisting of the sepals and petals. The former have a valvate aestivation, and each is supplied by a single median vascular strand with two smaller bundles on the sides consisting of a few phloem elements. The cells of the outer epidermis are very large and some of them grow out into hairy processes.

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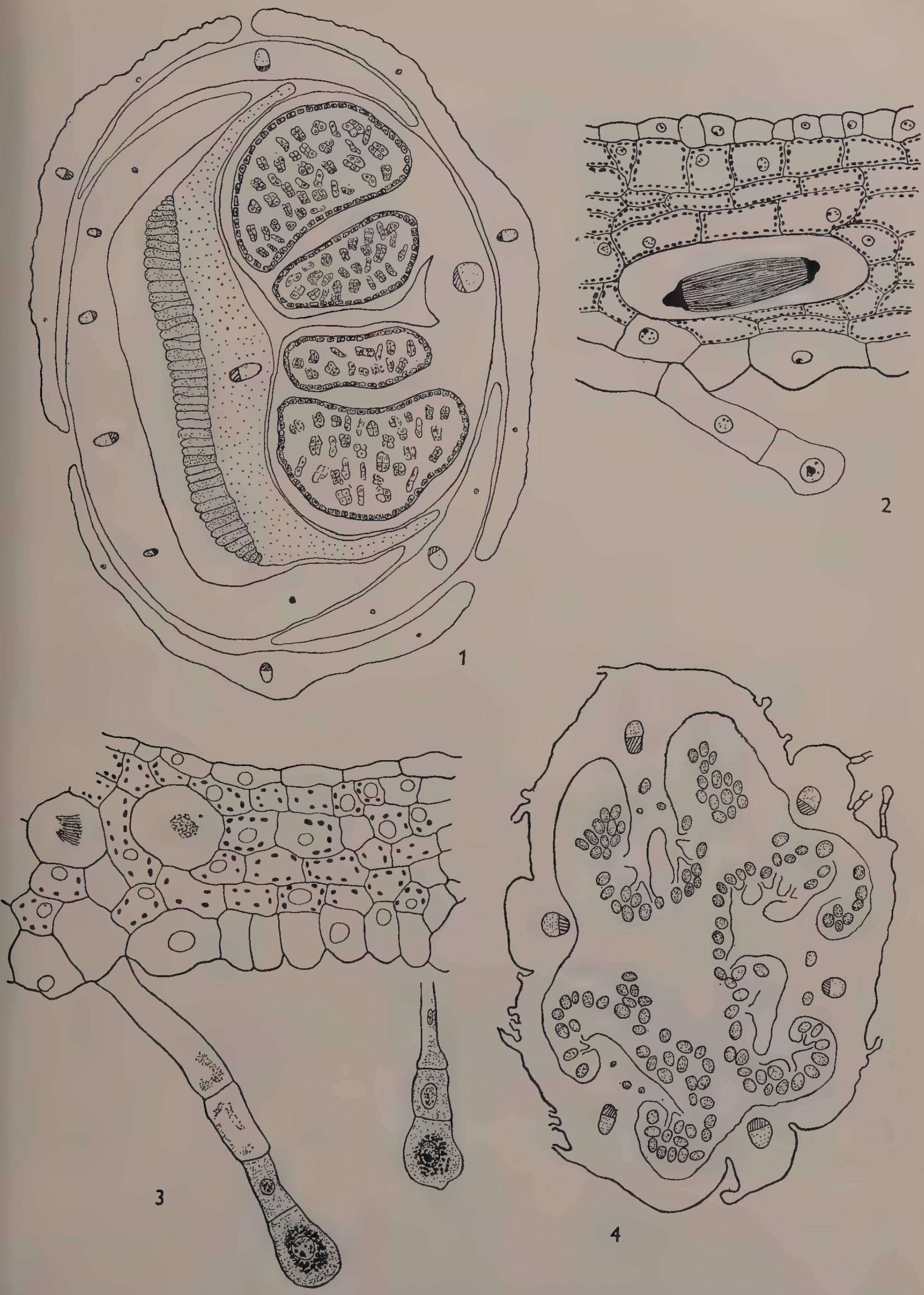
[1] I wish to record here my gratefulness to Dr C. R. Metcalfe, Keeper of the Jodrell Laboratory, who very kindly provided me with the facilities for completing the MS. during my stay at Kew Gardens in the summer of 1950 (P. Maheshwari).

[2] This work had been commenced several years ago when I was at the University of Dacca, but completed only after my joining the University of Delhi (P. Maheshwari).

[3] Such variation in one and the same species is very unlikely. See criticism by Schnarf (1929) and Maheshwari (1946).



Figs. 1–4. Fig. 1. T.S. flower showing outer and inner whorls of perianth, the fertile stamen and the rostellum. Each of the perianth segments has a single median vascular bundle and two smaller bundles, except the labellum which receives four to six bundles. × 70. Fig. 2. L.S. portion of ovary wall showing an enlarged cell containing raphides and a multicellular hair. × 375. Fig. 3. T.S. part of ovary wall showing uniseriate epidermal hairs with capitate terminal cells. Note two large mesophyll cells containing raphides. × 375. Fig. 4. T.S. ovary showing three parietal placentae bearing an indefinite number of ovules. × 40.

Between the inner and outer epidermis is a two- to three-layered mesophyll, some of whose cells are large and contain raphides. The other cells of the mesophyll contain numerous plastid-like bodies.

The two lateral petals are small, and their margins overlap those of the large central petal called the labellum. The lateral petals are similar in structure to the sepals, except that they have a six- to eight-layered mesophyll. The labellum is twelve- to fourteen-layered in the middle, but is thinner towards the margins. It is traversed by four to six vascular strands, while the lateral petals have only three strands. Some of the epidermal cells of the labellum are large and densely cytoplasmic. Cells containing raphides are present in the mesophyll, and plastids are abundant.

The single fertile stamen lies at the top of the 'column'. A cross-section of the flower passing through the anther is presented in Fig. 1.

The ovary is inferior, tricarpellary, syncarpous and unilocular (Fig. 4). Three forked parietal placentae arise from the ovary wall and become branched, each bearing numerous minute ovules at slightly varying stages of development. The ovary wall is six- to ten-layered. Excepting the outer and the inner epidermis, the intervening cells have plastids imbedded in the cytoplasm lining the cell walls. The cells containing raphides are large and irregularly distributed in the inner part of the ovary wall (Fig. 2). Uniseriate club-shaped hairs arise from the outer epidermis (Fig. 3). The terminal cell is large and capitate.

A transverse section of the ovary shows three prominent ridges, each with a single vascular strand. Alternating with them lie the three placentae. At the base of the placental tissue is a main vascular bundle accompanied by two or three smaller traces, the latter consisting mostly of phloem elements. Saunders (1937) describes the gynaecium of the Orchidaceae as consisting of six carpels arranged in two whorls, the outer consisting of three solid and sterile carpels and the inner of three semi-solid and fertile carpels. According to the classical view, which we prefer, the ridges represent the midribs and the three placentae are formed by a fusion of the margins of adjacent carpels.

Microsporogenesis and male gametophyte

The anther wall consists of an epidermis, an endothecium, two middle layers and the tapetum (Fig. 5). The tapetum is uninucleate.[1] By the time tetrad formation takes place the tapetum and the middle layers begin to degenerate (Fig. 6), and the endothecium develops the usual fibrous thickenings. When meiosis begins the microspore mother cells round up. Tetrads are of the decussate or tetrahedral type and the microspores do not separate from one another.[2] There is no synchronization of the divisions in the microspores belonging to different tetrads, but there is intratetrad synchronization. The generative cell is cut off towards the outer wall of each microspore but it soon moves to a more central position close to the tube nucleus. Figs. 7–15 represent the various stages of division in the development of the pollen grain.

The development of the male gametophyte is completed much earlier than that of the female. The generative cell is already formed in the anther, while the ovules are still at the megaspore mother cell stage.

Ovule

The young ovules arise as small protuberances on the placentae. As development proceeds, the funicle elongates and the ovules become anatropous.

The integuments are initiated at an early stage. Just after the archesporium is differentiated a slight protuberance is seen in the epidermal layer of the ovule and the cells in this region form the primordium of the inner integument. At the megaspore mother cell

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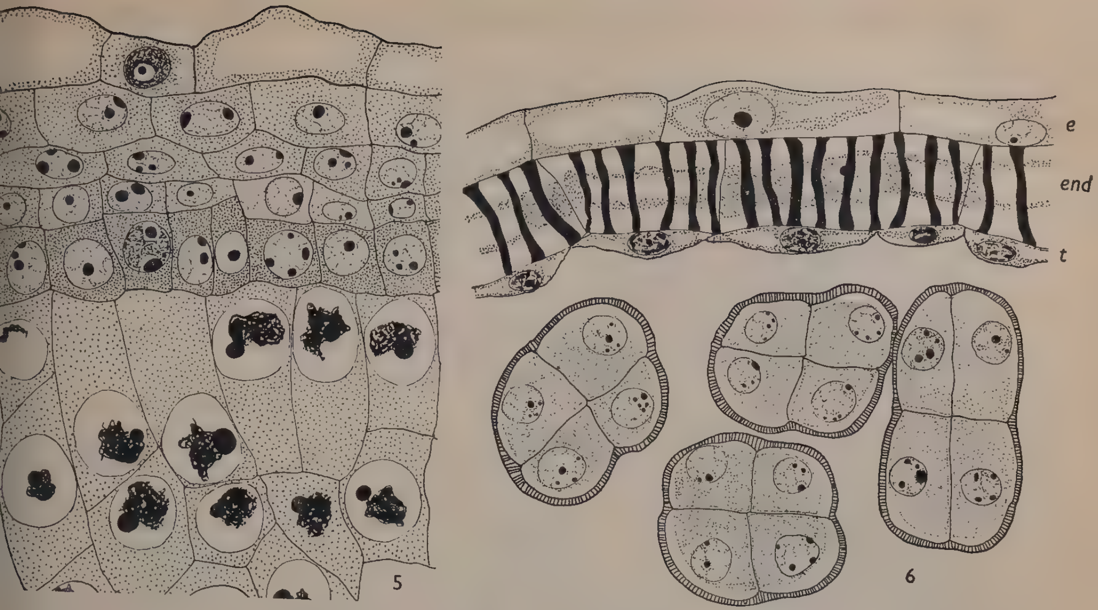
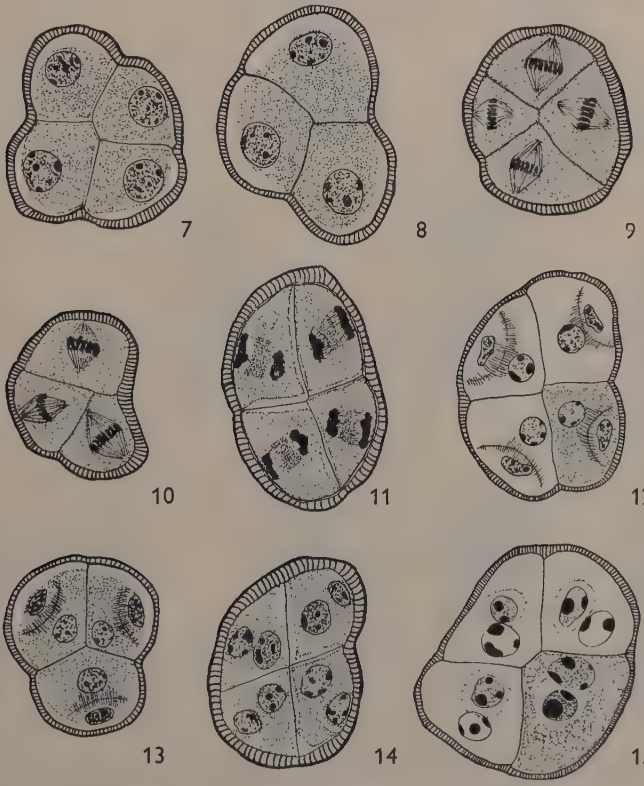
[1] This is the general condition in the family, the only exception being *Paphiopedilum druryi* which has a binucleate tapetum (Swamy, 1948).

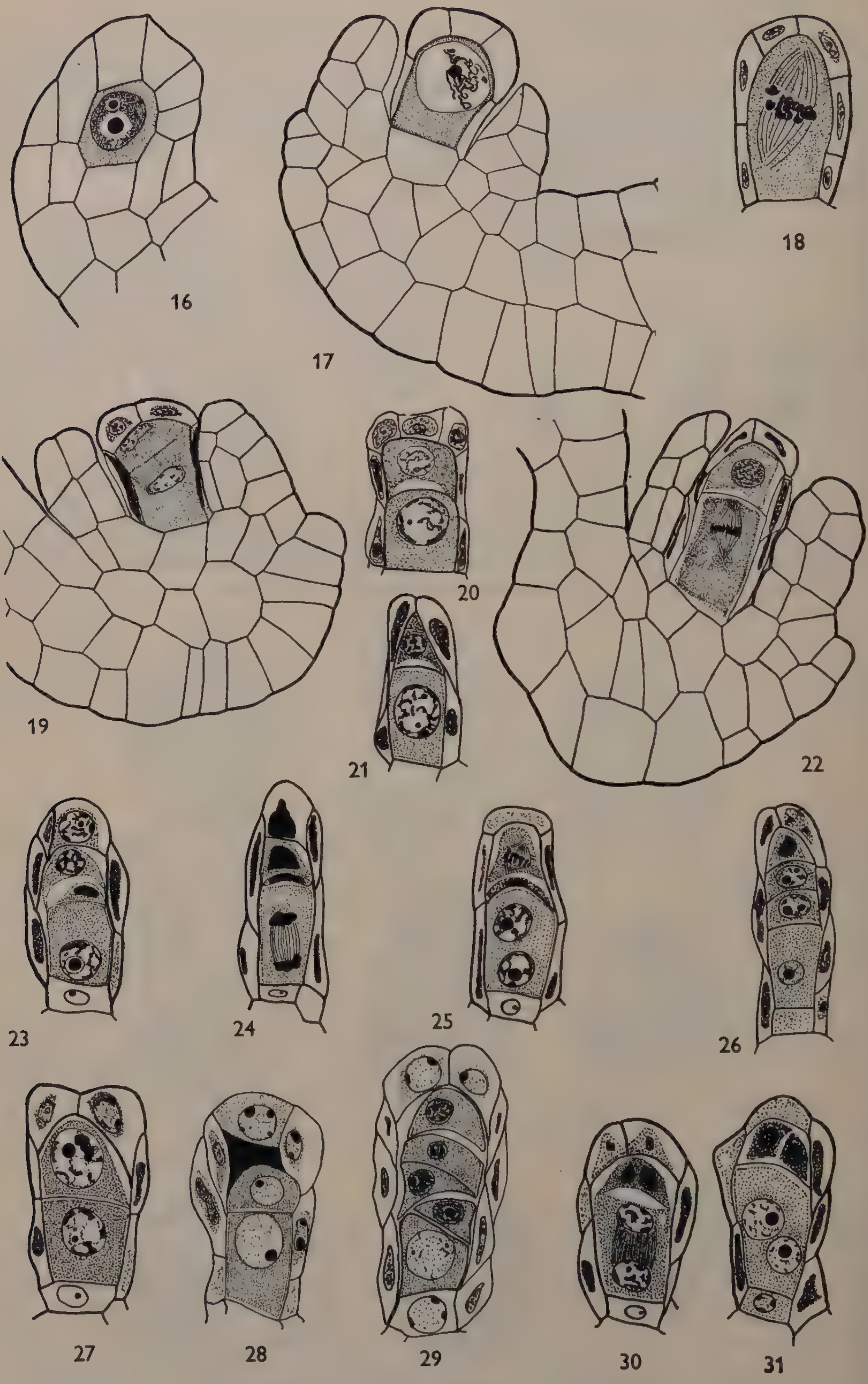
[2] Pace (1914) also found linear tetrads of microspores, but we have been unable to confirm it in our material.



Figs. 5, 6. Fig. 5. Portion of young anther showing epidermis (*e*), endothecium (*end*), two middle layers (*m′*, *m″*), uninucleate tapetum (*t*), and microspore mother cells in synizesis. Fig. 6. Older stage showing epidermis (*e*), fibrous endothecium (*end*), disintegrating tapetum (*t*), and tetrads of microspores. The middle layers have already disappeared. × 900.



Figs. 7–15. Fig. 7. Isobilateral tetrad of microspores. Fig. 8. Tetrahedral tetrad. Figs. 9, 10. Microspore nuclei in metaphase. Fig. 11. Telophase of division of microspores. Figs. 12, 13. Formation of cell plate between generative and vegetative nuclei. Fig. 14. Formation of vegetative and generative cells. Fig. 15. The generative cell has left its position near the wall and taken up a more central position. All × 900.



Figs. 16–31. For legends see p. 479.

stage it has already reached up to the level of the nucellar epidermis and become two-layered (Fig. 17). The outer integument, also two-layered, is differentiated soon afterwards (Fig. 19), but its growth seems to be arrested for some time. In post-fertilization stages, however, it grows more rapidly and soon protrudes beyond the inner integument.[1]

MEGASPOROGENESIS

The hypodermal archesporial cell (Fig. 16) functions directly as the megaspore mother cell without cutting off any parietal cell. The nucellus is greatly reduced, but one or two cells of the nucellar epidermis lying immediately above the megaspore mother cell or its derivatives often become greatly enlarged and vacuolated (Figs. 23, 24 and 27–29). Eventually, however, the nucellus disorganizes and the embryo sac is surrounded directly by the inner integument.

The nucleus of the megaspore mother cell is situated towards the upper part of the cell. Since the nuclear spindle is formed in the same position (Figs. 18, 19), the micropylar dyad cell is much smaller than the chalazal (Fig. 20). The former generally remains undivided and degenerates promptly (Fig. 21). In the lower dyad cell also the spindle is formed closer to the upper part (Fig. 22), resulting in the production of a small lenticular upper megaspore and a much larger lower megaspore. Thus a row of three cells is formed, composed of one dyad cell and two megaspores (Figs. 23, 24). Rarely the micropylar dyad cell may also divide (Fig. 25), resulting in the formation of four megaspores (Fig. 26).

We came across a few exceptions or abnormalities. Sometimes the spindle in the upper dyad cell is at right angles to the long axis of the ovule resulting in T-shaped tetrads, and in one or two cases no wall was noticed between the two megaspore nuclei formed by the lower dyad cell (Figs. 30, 31). If further development were to continue, the embryo sacs formed in this way would be bisporic.

Fig. 29 shows a linear row of five cells. Either the basal cell is the functioning megaspore and the 'pentad' arose by an extra division of one of the megaspores, or the four upper cells, all having a degenerated appearance, arose from the divisions of a single hypodermal megaspore mother cell, and the fifth cell is an accessory megaspore mother cell. Since two superposed megaspore mother cells do occur sometimes (Figs. 27, 28), we consider this to be the more probable explanation of the origin of the row of five cells.

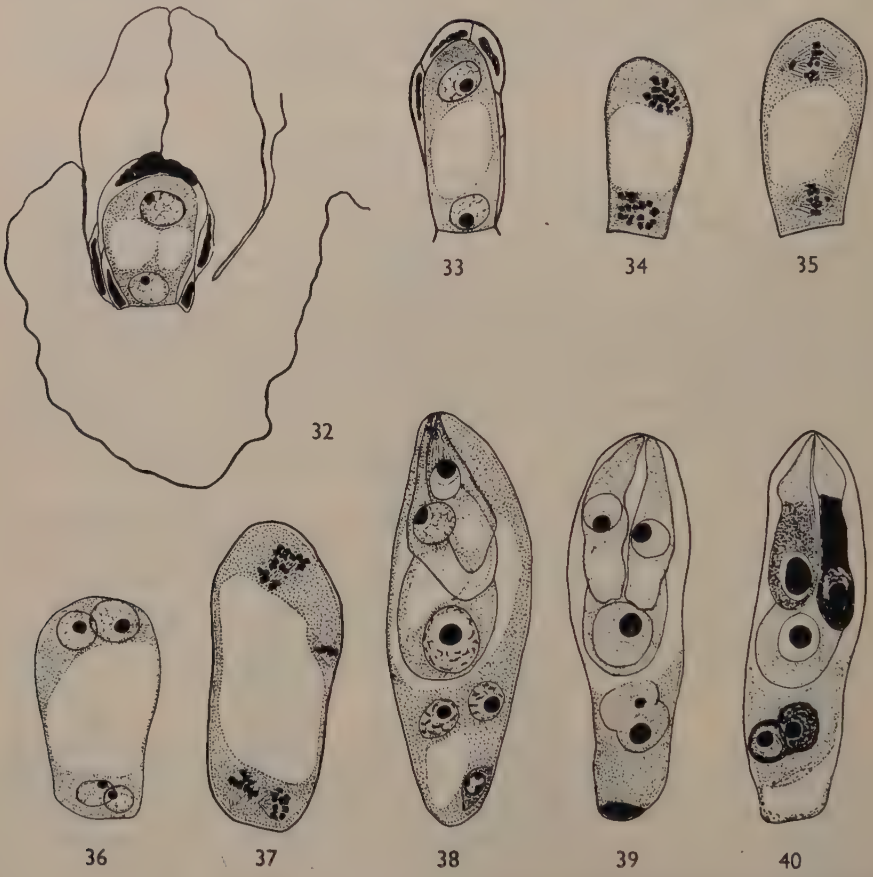
EMBRYO SAC

The nucleus of the functioning megaspore divides very early and leads on to the two-nucleate (Figs. 32, 33) and four-nucleate stages (Figs. 35, 36) which are quite normal. A few fortunate mitotic figures showed the haploid chromosome number to be 15 (Fig. 34). The remnants of the degenerated megaspores and the cells of the nucellar epidermis persist as darkly staining masses around the embryo sac (Fig. 32). Observations on a large number of ovules showed a frequent difference in the size of the nuclei, the two micropylar nuclei being slightly larger than the chalazal. After the four-nucleate stage, there is a third division. Fig. 37 suggests the formation of all eight nuclei, but a study of hundreds

[1] *P. insigne* (Afzelius, 1916) differs from other orchids in having a single integument.

Figs. 16–31. Fig. 16. L.S. nucellus showing hypodermal archesporial cell. Fig. 17. L.S. young ovule at megaspore mother cell stage showing origin of inner integument. Figs. 18, 19. Metaphase and telophase stages of meiosis I. Fig. 20. Dyad stage. Fig. 21. Upper dyad cell degenerating. Fig. 22. Division of the lower dyad cell, and initiation of outer integument. Fig. 23. Row of three cells consisting of the undivided upper dyad cell and two megaspores. One cell of the nucellar epidermis has enlarged. Fig. 24. Same, showing functional megaspore dividing. Fig. 25. Young two-nucleate embryo sac. Note belated division of the upper dyad cell. Fig. 26. Linear tetrad of megaspores. Fig. 27. Two superposed megaspore mother cells. Fig. 28. Upper megaspore mother cell has degenerated and the lower has divided to form two dyad cells. Fig. 29. A row of five cells; for explanation see text. Figs. 30, 31. Lower dyad cell dividing without wall formation. All × 900.

of embryo sacs has led us to conclude that this must be an exceptional condition and that as a rule the two chalazal nuclei remain undivided so that the mature embryo sacs are six-nucleate (see also Baranow, 1915).[1] Such a condition is not very infrequent in orchids (see Swamy, 1949*a*) and even five-nucleate embryo sacs originating because of a failure of division of the primary chalazal nucleus are known in *Gyrostachys gracilis* and *G. cernua* (Pace, 1914), *Orchis morio*, *Oncidium praetextum* (Afzelius, 1916), and *Cypripedium parviflorum* (Carlson, 1945).



Figs. 32–40. Fig. 32. L.S. ovule showing the two integuments, degenerating nucellus and two-nucleate embryo sac. Fig. 33. Embryo sac showing two nuclei separated by a large vacuole Figs. 34, 35. The two nuclei dividing. Fig. 36. Four-nucleate embryo sac. Fig. 37. The fou nuclei dividing. Fig. 38. Six-nucleate embryo sac showing two synergids, egg, two polar nucle and single antipodal cell. Figs. 39, 40. Six-nucleate embryo sac showing early degeneration o the single antipodal cell. All × 900.

The micropylar quartet forms the egg apparatus and upper polar nucleus, while the two nuclei at the chalazal end constitute the lower polar nucleus and a single antipodal cel (Fig. 38). The synergids, which are large pear-shaped structures with basal vacuoles project down to about one-third of the length of the embryo sac. Pace (1914) reports a filiform apparatus in *Gyrostachys gracilis*, but this was not distinct in our preparations most of which were made from material fixed in formalin acetic alcohol. The egg, which is

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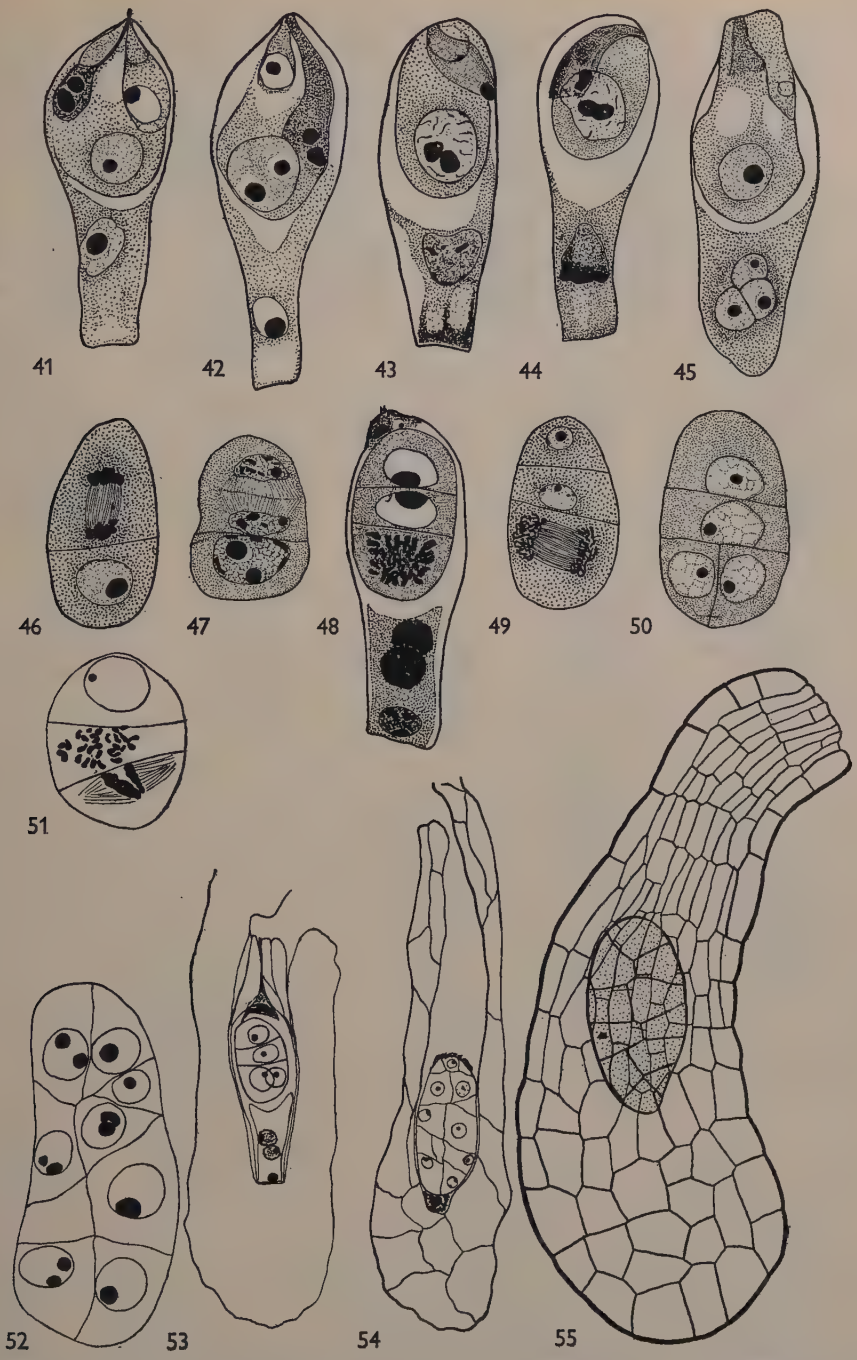
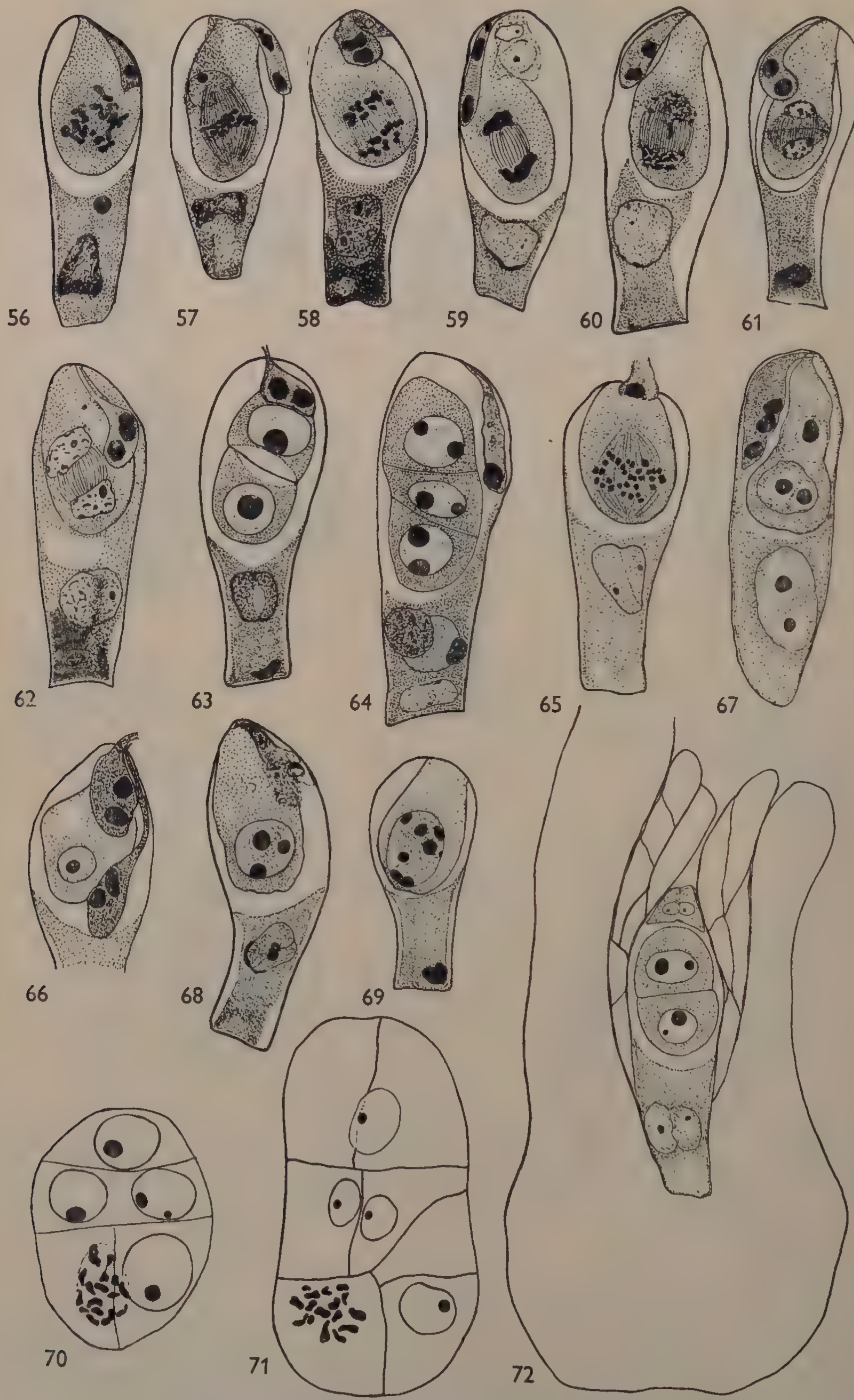
[1] A six-nucleate condition also originates sometimes by a fusion of the chalazal spindles during the last division, as in *Epipactis pubescens* (Brown & Sharp, 1911) and *Paphiopedilum insigne* (Afzelius 1916), or by the early degeneration of two nuclei of the chalazal quartet.



Figs. 41–55. Fig. 41. Embryo sac with pollen tube closely appressed to egg; one of the synergids has disorganized. × 900. Figs. 42–44. Stages in syngamy. × 900. Fig. 45. Embryo sac showing zygote and three fusing nuclei, of which two are the polars and the third may be a male nucleus or the nucleus of an antipodal cell. × 900. Figs. 46–52. Stages in development of pro-embryo. × 900. Fig. 53. L.S. ovule showing disintegration of cells of inner integument excepting those lying at the tip. × 240. Fig. 54. L.S. ovule showing virtual disappearance of inner integument; embryo enclosed inside outer integument. × 240. Fig. 55. Surface view of seed showing embryo enclosed within the seed coat formed by the outer integument. × 240.



Figs. 56–72. For legends see p. 483.

larger than the synergids, projects beyond the latter and reaches down to the middle of the embryo sac. Immediately below it are situated the two polar nuclei which may not fuse or fuse just at the time of fertilization. The antipodal cell degenerates very early and is soon almost unrecognizable (Figs. 39, 40).

FERTILIZATION

Usually a single pollen tube enters the ovule. Its free end swells and becomes closely appressed to one side of the egg (Fig. 41). The two sperms are spherical and take a very dense stain. The tube nucleus is frequently not discernible, and it is possible that it disintegrates somewhere in the pollen tube. In *Platanthera* also, Hagerup (1947) reports that the swollen tip of the pollen tube sometimes contains only the two male nuclei.

At times three nuclei of similar size were observed inside the pollen tube (Fig. 62). One of these is probably the tube nucleus. More often, however, it is smaller than the male gametes and occupies the narrow hinder part of the pollen tube (Fig. 59).

The pollen tube enters through the micropyle, and one of the synergids is disorganized in the process. Syngamy (Figs. 42–44) takes place, but triple fusion is delayed or is omitted altogether. Frequently the second male gamete destined to fuse with the polar nuclei remains behind in the pollen tube and is never discharged from it.

ENDOSPERM AND EMBRYO

The polar nuclei may either degenerate before fusion (Fig. 48) or after fusion has taken place to form the secondary nucleus (Figs. 43, 44). As far as we have been able to observe, triple fusion does not occur as the second male gamete is seldom discharged. Even when fusion does take place (Fig. 45),[1] the development does not proceed further. This is in accordance with the condition observed in the majority of orchids. It is only in certain species of *Cypripedium*, *Paphiopedilum*, *Chamaeorchis* (Afzelius, 1916) and *Vanilla* (Swamy, 1947) that a few endosperm nuclei are formed, but even these are ephemeral. In *Spiranthes* the shrivelled and densely staining secondary nucleus can be seen in the basal part of the embryo sac just below the zygote or the developing pro-embryo (Fig. 54).

The zygote divides transversely to form a two-celled pro-embryo. The upper or basal cell undergoes another transverse division (Figs. 46, 47) followed by a vertical division of the terminal cell (Figs. 48–50 and 53). The embryo sac is small, and the developing embryo occupies almost the entire space inside it. Further divisions (Figs. 51, 52) follow the sequence observed in the sexual race of *S. cernua* (Swamy, 1948) and in *Achroanthes monophylla* (Stenar, 1937). The cells of the inner integument undergo degeneration at this stage (Figs. 53, 54). Leavitt (1901) and Swamy (1948) have reported the occurrence of polyembryony in *Spiranthes cernua*, but in our plant only a single embryo was formed in each seed.

[1] It is possible, of course, that the third nucleus in this figure is not the male nucleus at all but the single antipodal.

Figs. 56–72. Fig. 56. Embryo sac showing haploid egg cell in division; one male nucleus is in the pollen tube and the other is lying just above the degenerating secondary nucleus. Fig. 57. Embryo sac showing metaphase stage in egg while pollen tube has not yet discharged its contents. Fig. 58. Egg in anaphase stage showing haploid number of chromosomes ($n=15$). Figs. 59, 60. Telophase. Figs. 61–63. First division of unfertilized egg completed. Fig. 64. Embryo sac showing three-celled pro-embryo; the presence of two nucleoli in cells of pro-embryo seems to indicate that it arose from a fertilized egg. Note the tube nucleus inside pollen tube and belated triple fusion. Fig. 65. Embryo sac showing division of fertilized egg with diploid number of chromosomes. Fig. 66. Embryo sac with two pollen tubes still unburst. Fig. 67. Embryo showing fertilization; note second pollen tube with nuclei still undischarged. Fig. 68. Embryo sac showing fertilization of egg by both male nuclei. Fig. 69. Embryo sac showing egg surrounded by several male nuclei. Figs. 70, 71. Pro-embryos showing haploid number of chromosomes. Fig. 72. Embryo sac showing parthenogenetic pro-embryo; note the intact synergids. All × 900.

MATURE SEED

During post-fertilization stages the outer integument grows considerably beyond th inner, while the inner integument degenerates and disappears leaving only a membranou covering over the embryo (Figs. 53, 54). In some cases the nucellar cells at the chalaz also degenerate, resulting in the formation of a small cavity just below the embryo sa A similar structure of the seed has been described by Carlson (1940) in *Cypripedium* an Baranow (1915) in *Serapias*. The embryo remains undifferentiated even in the matur seed (Fig. 55).

PARTHENOGENESIS, POLYSPERMY AND OTHER ABNORMALITIES

Recent studies by Hagerup (1944, 1945, 1947) on *Orchis*, *Epipactis*, *Listera* and *Cephalanthera* have shown that a small percentage of the embryos develop parthenogenetically and sometimes polyploid embryos result by a fusion of the egg with more than on sperm (polyspermy).

Examination of a large number of ovules of the material under study revealed simila peculiarities. In such embryo sacs either the pollen tube had failed to open or, if it ha discharged its contents, the male nuclei lay unused (Figs. 57–63). Chromosome count in the dividing egg or the pro-embryos showed the haploid number (±15) in the unfertilized (Figs. 56–58, 70 and 71) and diploid number (±30) in the fertilized embryo sac (Figs. 51, 65).

Parthenogenetic embryos were also seen in a few embryo sacs that had apparently no received a pollen tube at all. In one such embryo sac the synergids were still intac (Fig. 72).

Rarely more than one pollen tube was found to penetrate the embryo sac (Fig. 66) In some cases the supernumerary pollen tube or tubes remained unused (Fig. 67), or th male nuclei of several tubes were released in the embryo sac. Fig. 69 shows an embryo sa in which six male nuclei are lying over the egg. Such a condition could have resulte either from the entry of more than one pollen tube inside the ovule or by repeated division of the generative nucleus of the same pollen tube. Unfortunately the preparation was no good enough to make a definite decision on that point. It may be added that while n case of polyspermic fertilization was actually observed by us, the possibility of its occurrence cannot be denied. Hagerup (1944, 1945, 1947) also mentions similar cases in *Orchis* *Epipactis* and some other orchids.

DISCUSSION

The tribe Spirantheae includes sixteen genera of which only five have been studie embryologically, viz. *Neottia*, *Zeuxine*, *Listera*, *Goodyera* and *Spiranthes*. In *Neotti* (Modilewski, 1918), which is a saprophytic form, the embryo sac is of the *Allium* type bu the last division is omitted in the chalazal end so that only six nuclei are formed. I *Goodyera* (Afzelius, 1916) the embryo sac is of the *Polygonum* type. Hagerup's (1947 account of the development of the embryo sac of *Listera ovata* is not very clear. He say that no antipodals are formed and 'the mature embryo sac merely seems to contai 4 nuclei'.[1] He records the occurrence of parthenogenesis, polyspermy and synergid embryo in his material collected from the environs of Copenhagen. In *Zeuxine sulcata* (Swamy 1946) the pollen grains and embryo sacs are sterile and adventive embryos arise from th cells of the nucellar epidermis. The genus *Spiranthes* has been studied by several workers Leavitt (1901), Pace (1914), Baranow (1915) and Swamy (1948). Their observations hav already been reviewed on p. 474.

Coming to *S. australis*, the chief features in its embryology are summarized below

Microsporogenesis occurs as usual, the pollen grains remain united in tetrads, and eac grain is bicelled at maturity.

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[1] Tuschnjakowa (1929) figures an eight-nucleate embryo sac in this species, and it is likely tha Hagerup missed some of the nuclei.

The embryo sac is of the *Polygonum* type and arises from the chalazal megaspore of the tetrad. However, due to a failure of the last division at the chalazal end, it contains only six nuclei organized to form an egg, two synergids, two polar nuclei and a single antipodal cell. The pollen tube enters through the micropyle. One of the male gametes fuses with the egg. The other may remain unused; and even if triple fusion occurs, the primary endosperm nucleus disintegrates without undergoing further divisions. The ovoid and undifferentiated embryo lacks a well-marked suspensor, and is enclosed within the seed-coat formed only by the outer integument. An important point is that sometimes the egg may develop parthenogenetically. The following facts may be cited in support of this:

(1) In some embryo sacs, although the pollen tube had not opened, the egg had already divided and formed a two-celled pro-embryo.

(2) In certain embryo sacs, although the pollen tube had discharged its contents, the male nuclei remained unused. Nevertheless, embryo formation had begun.

(3) An embryo had developed in one embryo sac, which had apparently not received a pollen tube at all and in which the synergids were still intact.

(4) Chromosome counts during the first division showed the haploid number (±15) in parthenogenetic eggs and diploid number (±30) in the fertilized eggs.

(5) Embryos in unfertilized embryo sacs showed the haploid number of chromosomes, while embryos in fertilized embryo sacs showed the normal diploid complement.

It is interesting to note that haploid embryos have also been recorded by Hagerup (1944, 1945, 1947) in some other orchids, viz. *Orchis*, *Epipactis*, *Listera* and *Cephalanthera*. Careful study may reveal their occurrence in other members of the family.

Rarely two pollen tubes were found in an embryo sac and in one case six male nuclei were seen around the egg. This indicates the possibility of polyspermic fertilization and the origin of polyploid embryos.

Swamy (1948) has recorded the occurrence of three different races in *Spiranthes cernua*: one being normal, another showing adventive embryony, and a third being intermediate. Although the Dacca and Nepal collections of *S. australis* have not revealed the variability found in *S. cernua*, the occurrence of parthenogenetic development in our plant is of interest as indicative of a tendency towards apomictic development in the genus *Spiranthes*.

SUMMARY

The flower comprises two trimerous whorls of perianth lobes, of which the labellum is supplied by four to six vascular strands and the rest by three bundles each. Some of the mesophyll cells become enlarged and contain raphides.

The fertile stamen is quadrilocular. At the tetrad stage only the epidermis and the fibrous endothecium persist, while the two middle layers and tapetum disintegrate. The tapetal cells are uninucleate and the microspores remain together in tetrads. The pollen grains are bicelled at the time of shedding.

The tricarpellary inferior ovary bears an indefinite number of bitegmic anatropus ovules arising from three parietal placentae. The hypodermal archesporial cell differentiates directly into the megaspore mother cell which gives rise to a linear tetrad of megaspores. The upper dyad cell rarely degenerates before the division is completed. In one instance a row of five cells was noticed. This might have arisen from two superposed megaspore mother cells or from an extra division of one of the megaspores.

The chalazal megaspore functions. The mature embryo sac is usually six-nucleate, probably due to a suppression of the last division of the two chalazal nuclei. The single antipodal cell degenerates early and may not be seen in mature embryo sacs. The two polar nuclei may fuse to form the secondary nucleus or degenerate without fusion.

Syngamy occurs, but triple fusion is delayed or is omitted altogether so that there is no endosperm formation. The first division of the egg is transverse. The mature embryo is ovoid in shape and undifferentiated. It has no suspensor haustoria and is enclosed within the seed coat formed by the outer integument.

Various abnormalities have been recorded. Evidence is presented to indicate that parthenogenetic development of the egg is possible and does occur in some ovules. In such embryo sacs the undischarged pollen tube is usually seen beside the egg, but parthenogenetic embryos have also been observed in embryo sacs that had apparently not received a pollen tube at all. These observations have been confirmed by chromosome counts during division stages of the egg as well as in cells of the pro-embryo. Occasionally an embryo sac receives more than one pollen tube. Both the male nuclei of a pollen tube or the male nuclei of different pollen tubes may fertilize the egg, indicating the possibility of polyploid embryos.

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A revision of the African species of Blechnum. By E. A. C. L. E. Schelpe

(With 5 Text-figures)

[Read 25 October 1951]

Much confusion has arisen in herbaria in the identification of some of the African species of *Blechnum*, especially in the distinction between some of the South African species. In this revision, an attempt is made to define the limits of variability of the species concerned, following an extensive study of the plants in their natural habitats.

Material of the African species in the Linnaean Herbarium, the herbaria at the British Museum (Nat. Hist.) and the Royal Botanic Gardens, Kew, and various herbaria in South Africa and elsewhere, has been examined by the author. The specimens examined are cited in this paper. Unfortunately, the author has not had access to some type material.

A great part of the herbarium material examined consisted of sterile fronds, which are of more common occurrence in the field. Consequently, the key to the species has been based on the characters of the sterile fronds. The spore dimensions given in this paper are the averages of measurements made of the lateral views of as many spores as possible. The spores measured had been mounted dry in Canada Balsam. Bower (1928) regarded the spores of *Blechnum* as having no perispores, misquoting Hannig (1911), who found perispores to occur in *Blechnum arborescens*. Apparently this was the only species of this genus whose spores Hannig examined. Perispores occur in all the African species of *Blechnum* except *B. australe* and *B. punctulatum*, together with their varieties and forms (Fig. 5).

In the descriptions of the species, the dimensions and descriptions of the pinnae given, apply only to the pinnae in the middle portion of the frond. Figures given for the length of fronds do not include the stipe length. The figures given for rhizome diameters are, in fact, diameters of the rhizome proper together with old stipe bases and paleae. Useful key characters appear in italics in the descriptions. The localities of South African collections are listed under the magisterial divisions in which they occur.

Only one of the non-African blechnoid ferns has apparently escaped from cultivation in Africa. This is *Doodia media* R.Br., an Australasian fern which has been found in the environs of Pietermaritzburg. It may be distinguished from the African *Blechnum* species by its small sharply serrate pinnae and the row of areolae formed on either side of the pinna midrib by anastymosis of the lowest veinlets. The geographical areas considered in this revision include the African continent, Fernando Po and São Tomé.

KEY TO THE AFRICAN SPECIES OF *BLECHNUM*

Bases of all sterile pinnae adnate to the rachis.
  Stipe and rachis minutely but densely papillose; sterile pinnae dark green with crenulate margins. 4. *B. ivohibense.*
  Stipe and rachis smooth.
    Upper surface of rachis of sterile frond convex; mid-frond sterile pinnae oblong, 2–4 cm. long, 0·4–0·6 cm. broad, apices rounded. 1. *B. inflexum.*
    Upper surface of rachis of sterile frond, concave, channelled; mid-frond sterile pinnae lanceolate oblong to attenuate, 4–18 cm. long, 0·7–2·0 cm. broad.
      Stipe wholly black or lower half black. 2. *B. nudum.*
      Stipe brown or pale brown.
        Sterile pinnae with unequally cuneate bases wholly or partly adnate to the rachis, apex acute, coriaceous; frond not markedly decrescent. 5. *B. tabulare.*
        Sterile pinnae widened to a wholly adnate base, apex acuminate; frond markedly decrescent below. 3. *B. attenuatum* and var.

Bases of middle and lower sterile pinnae not adnate to the rachis; lower pinnae subsessile or petiolate.

Margins of sterile pinnae finely serrate. **6.** *B. capense.*

Margins of sterile pinnae entire, crenate or irregularly pinnatifid.

Sterile pinnae mucronate, oblong to lanceolate, firmly membraneous to subcoriaceous; basal auricular lobes of lower sterile pinnae usually mucronate. **8.** *B. australe.*

Sterile pinnae not mucronate, lanceolate; basal auricular lobes of sterile pinnae rounded. **7.** *B. punctulatum* and vars.

(1) **Blechnum inflexum** (Kunze) Kuhn

Blechnum inflexum (Kunze) Kuhn, *Fil. Afr.*, 92 (1868); Christensen, *Ind. Fil.* 155 (1906); Sim, *Ferns S. Afr.* ed. ii, 178, t. 74 (1915). *Lomaria inflexa* Kunze, *Linnaea*, **18**, 117 (1844); *Farrnkrauter*, t. 65 (1840–47); Pappe & Rawson, *Syn. Fil. Afr. Austr.*, 28 (1858); Hook., *Sp. Fil.* **3**, 37 (1860); Sim, *Ferns S. Afr.* ed. i, 116 (1892). *Lomaria discolor* (Forst.) Keys. var. *natalensis* Bak., *Syn. Fil.* ed. ii, 481 (1874).

Rhizome erect to suberect, up to 10 cm. long, 2–3 cm. diameter, paleaceous; rhizome scales lanceolate, brown, 0·2–0·5 cm. long. **Stipe** light brown to *brown*, not channelled, glabrous, 1–5 cm. long. **Frond** pinnate: sterile frond lanceolate, 15–25 cm. long, 4–6 cm. broad, somewhat reduced below; fertile frond linear lanceolate, 13–20 cm. long, 3–5 cm. broad, erect. **Rachis** light brown, *not channelled*, glabrous. **Pinnae**: sterile pinnae *oblong*, entire, 2·5–3·6 cm. long, 0·4–0·7 cm. broad, subcoriaceous, apex rounded to broadly acute, base broadened wholly adnate to the rachis; fertile pinnae linear oblong, 2·0–2·8 cm. long, 0·4–0·6 cm. broad, subsessile. **Sori** linear, lomarioid, extending almost the length of the fertile pinna; indusium, 0·2 cm. broad, torn at maturity. **Spores** greenish brown, $58{\cdot}8\mu \times 39{\cdot}6\mu$, enclosed by a perispore.

Although the sterile pinnae in most specimens are discrete, they may overlap in some specimens. The fact that the rachis of the sterile frond is convex on the upper surface may be used in separating this species from *B. nudum*. The depth of the brown coloration at the base of the stipe is variable and may increase with age. However, the stipe base is not black as in *B. nudum* nor is it ever wholly black.

HABITAT

B. inflexum usually occurs on stream banks under little or no shade. It may also be found in moist localities about forest margins or occasionally about boulder bases in grassland in the Drakensberg at about 6000 ft. altitude. This appears to be its upper altitude limit in Natal. The lower altitude limit of the species in the eastern region of South Africa is about 2000 ft.

TYPE LOCALITY

'Ad portum Natalensem': *Gueinzius s.n.* (1842) in Herb. Kunze. In view of the known distribution of this species, it is probable that the type specimen was collected at some locality fifty miles or more from the coast. The type specimen, at Leipzig, was destroyed during the war.

DISTRIBUTION

CAPE PROVINCE

King Williams Town: Perie, *Flanagan 24* (PRE), *Holland s.n.* (CTK), *Sim s.n.* (BOL, PRE, TRV).

NATAL

Bergville: Natal National Park, *Bottomley s.n.* (PRE), *Cliver 477* (NH), *Schelpe 2003* (BM). **Estcourt**: Drakensberg, *Buchanan s.n.* (K). **Impendhle**: Impendhle, *Clarkson 145* (BM, NU). **Lions River**: Balgowan, *Mogg 3814* (PRE); Karkloof, *Rycroft 545* (NU);

Nottingham Road, *Edwards 121* (NU), *D. Smith 155, 156* (NU). **Nkandhla**: Qudeni, *Allsopp 766* (NU), *Clarkson 82* (NU), *Fisher 832* (NU, PRE). **Polela**: Bulwer, *Allsopp 849* (NU), *Clarkson 189* (NU); Drakensberg Gardens Area, *Schelpe s.n.*; Underberg, *McClean 685* (NU).

Locality unknown: *Cooper 2934* (K), *McKen s.n.* (K).

TRANSVAAL

Belfast: Dullstroom, *Taylor s.n.* (BOL).

(2) **Blechnum nudum** (Labill.) Mett. ex Luerss.

Blechnum nudum (Labill.) Mettenius ex Luerssen, *Flora, 1876*, 292 (1876); Wakefield, *Victorian Naturalist*, **59**, 193 (1943). *Onoclea nuda* Labill., *Pl. Nov. Holl.*, 96, t. 245 (1806). *Lomaria nuda* (Labill.) Willd., *Sp. Pl.*, **5**, 289 (1810); Lowe, *Ferns*, **4**, 127, t. 51 (1872). *Stegania nuda* (Labill.) R.Br., *Prod. Fl. Nov. Holl.*, 153 (1810). *Stegania falcata* R.Br., *Prod. Fl. Nov. Holl.*, 153 (1810). *Lomaria falcata* (R.Br.) Spreng., *Syst. Veg.*, **4**, 62 (1827). *Lomaria discolor* (Forst.) Willd. var. *nuda* (Labill.) Bak., *Syn. Fil.*, 481 (1874). *Blechnum discolor* (Forst.) Keys. in part: C. Chr., *Ind. Fil.*, 153 (1906); Ewart, *Fl. Victoria*, 51, fig. 15 (1930); Black, *Fl. S. Austr.*, ed. ii, 37 (1943). *Lomaria discolor* (Forst.) Willd. in part: Hook., *Sp. Fil.*, **3**, 3 (1860); Bentham, *Fl. Austr.*, **7**, 735 (1878); Bailey, *Queensl. Fl.*, **6**, 1964 (1902); Rodway, *Tasm. Fl.*, 283 (1903).

Rhizome erect to suberect, up to 16 cm. long, 3·5–4·0 cm. diameter, paleaceous; paleae linear lanceolate, 0·5–2·5 cm. long, dark brown to black. **Stipe** *black* for the whole length or the lower half, glabrous, channelled, 5–14 cm. long. **Frond** pinnate: sterile frond lanceolate, erect glabrous, firmly membraneous to coriaceous, 22–44 cm. long, 8–17 cm. broad, hardly reduced below; fertile frond lanceolate oblong, erect, 15–40 cm. long, 3–6 cm. broad. **Rachis** black on the ventral surface or all brown, light brown on the dorsal surface, *channelled*, glabrous. **Pinnae**: sterile pinnae oblong lanceolate, entire or minutely crenulate towards the apices, 4–9 cm. long, 0·6–1·0 cm. broad, firmly membraneous to coriaceous, apex acute-acuminate to rounded, base wholly adnate to the rachis; fertile pinnae linear, 2–4·5 cm. long, 0·2–0·4 cm. broad, sometimes falcate, subsessile, apex acute. **Sori** linear, lomarioid, extending almost the length of the fertile pinnae; indusium brown, torn at maturity, 0·1 cm. broad. **Spores** brown, $44{\cdot}4 \times 30{\cdot}0\,\mu$.

Wakefield (1943) drew attention to the fact that *B. discolor* and *B. nudum* were distinct species. *B. nudum* lacks the ferrugineous colouring of the ventral surface of the frond, exhibited by *B. discolor*, and also lacks the semi-persistent reddish-brown hair-like scales frequently seen on the rachises of *B. discolor*. In *B. nudum* the fertile pinnae are subsessile, whereas in *B. discolor*, the pinna bases are adnate to the rachis and considerably widened (up to 1·6 cm. wide), the widened portion exhibiting a greater sterile area towards the base of the frond (cf. Lowe, *Ferns*, **4**, t. 56). *B. discolor* appears to be limited in its distribution to New Zealand.

Of the three collections of plants from South Africa regarded here as *B. nudum*, only one (*Schelpe 1866*) closely resembles the majority of the Australian and Tasmanian specimens. In this plant the stipe is completely black, the dark coloration extending up the ventral surface of the rachis. Also the pinnae do not overlap, are widened abruptly to an adnate base and have acute-acuminate apices. The plant was found on the shaded floor of Kloof forest. In the two other collections (*Schelpe 1979* and *Pillans 9595*) only the lower half of the stipe is black, the upper half being pale brown. The pinnae in both overlap and, although having wholly adnate bases, they are somewhat auriculate, being widened and then narrowed to the base. The pinna apices are rounded to rounded-acute. In all these collections the dorsal surface of the rachis is markedly channelled. The difference in the extent of the dark coloration up the stipe and rachis is wider among these three South African specimens than that observed among numerous Australasian plants.

The few spores obtained from the single very old fertile frond collected in the Cedarberg (*Schelpe 1979*) were not significantly different in size from those obtained from Australian specimens. However, they lacked the large perispores which occur in the Australian plants (Fig. 5). It is possible that the perispores might have been lost in these old spores, since a proportion of the spores shaken out of herbarium material from Australia had either lost their perispores or were in the process of doing so.

Although there is little doubt that the plants of the first collection (*Schelpe 1866*) are *B. nudum*, the plants in the other two South African collections may constitute a group distinct from typical *B. nudum*. Considering the differences in the habitats of these three collections, all three are regarded as falling within the range of epharmonic variation of *B. nudum*, pending the collection of further material.

HABITAT

Plants of *B. nudum* were first found in South Africa by the author in Lange Kloof, Jonkershoek Valley near Stellenbosch. They grew in small colonies on a steep stream bank in the shade of forest trees, at about 500 ft. altitude. A colony of the supposed xeromorphic form was discovered in a sandy exposed stream bed among boulders on the Middelberg Ridge of the Central Cedarberg at about 4500 ft. altitude.

TYPE LOCALITY

Van Diemen's Land (Tasmania).

DISTRIBUTION

CAPE PROVINCE

Ceres: Schwefteberg, *Pillans 9595* (BOL). **Clanwilliam**: Cedarberg, Boskloof, *Schelpe 1979* (BOL). **Stellenbosch**: Jonkershoek, Lange Kloof, *Schelpe 1866* (BM, BOL).

(3) **Blechnum attenuatum** (Sw.) Mett.

Blechnum attenuatum (Sw.) Mett., *Fil. Hort. Bot. Lips.*, 64, t. 3, f. 1–6 (1856); Christ, *Farnk. d. Erde*, 181 (1897); Engl. & Prantl, *Nat. Pfl.*, **1**, 4, 247 (1902); C. Chr., *Ind. Fil.*, 151 (1906); Sim, *Ferns S. Afr.*, ed. ii, 179, t. 75 (1915). *Onoclea attenuata* Sw., *Schrad. J.*, *1800*, 2, 73 (1801). *Lomaria attenuata* (Sw.) Willd., *Sp. Pl.*, **5**, 290 (1810); Kunze, *Linnaea*, **18**, 116 (1844); Pappe & Rawson, *Syn. Fil. Afr. Austr.*, 28 (1858); Hook., *Sp. Fil.*, **3**, 6 (1860); Hook., *N.Z. Fl.*, 368 (1864); Lowe, *Ferns*, **4**, t. 64 (1872); Hook. & Bak., *Syn. Fil.*, 176 (1874); Bentham, *Fl. Austr.*, **7**, 736 (1878); Sim, *Ferns S. Afr.*, ed. i, 118 (1892). *Lomaria acuminata* Desv., *Mag. d. Ges. Naturf. Fr. Berl.*, **5**, 326 (1811). *Lomaria heterophylla* Desv., *Mag. d. Ges. Naturf. Fr. Berl.*, **5**, 330 (1811); Kunze, *Linnaea*, **10**, 506 (1836); Pappe & Rawson, *Syn. Fil. Afr. Austr.*, 27 (1858). *Lomaria gigantea* Klf., *Enum. Fil.*, 150 (1824); Hook., *Sp. Fil.*, **3**, 10 (1860). *Lomaria hamata* Klf., *Enum. Fil.*, 150 (1824). *Blechnum giganteum* (Kaulf.) Schlecht., *Adumb.*, 36, t. 20, 22 (1827). *Blechnum heterophyllum* (Desv.) Schlecht., *Adumb.*, 36 (1827). *Lomaria circinnata* Boj., *Hort. Maur.*, 406 (1837). *Lomaria decipiens* Pappe & Rawson, *Syn. Fil. Afr. Austr.*, 27 (1858). *Spicanta attenuata* (Sw.) O. Ktze., *Rev.*, 821 (1891).

Rhizome procumbent, up to 45 cm. long, 2·0–3·4 cm. diameter, paleaceous, paleae subulate, 1·2–4·2 cm. long, 0·1–0·3 cm. broad, dark brown, sometimes spirally twisted when dry. **Stipe** light brown, channelled, 5–18 cm. long, glabrous. **Frond** pinnate: sterile frond pinnate, occasionally bipinnatifid, suberect or arching, lanceolate, glabrous, thinly coriaceous, 40–180 cm. long, 8–22 cm. broad, *markedly reduced below*; fertile frond pinnate, lanceolate, glabrous, 40–160 cm. long, 7–20 cm. broad, reduced below. **Rachis** light brown, glabrous. **Pinnae**: sterile pinnae linear-lanceolate, entire or occasionally irregularly pinnatifid or slightly undulate, with a narrowly reflexed margin, 3–18 cm. long, 1·0–1·8 cm. broad, base abruptly widened, wholly adnate to the rachis, apex acuminate; fertile pinnae linear, 4–14 cm. long, 0·3–0·4 cm. broad, sessile, with a broadened base adnate to the rachis, often recurved or pendant. **Sori** linear, lomarioid, extending almost the length of the fertile pinna; indusium, 0·1 cm. broad, torn at maturity. **Spores** light brown, 53·9 × 32·8 μ, enclosed in a perispore.

Individuals of this species with bipinnatifid fronds have occasionally been found in widely separated localities. A colony of such individuals was seen by the author at Macmac, Transvaal, and it was found that many, but not all, of the adult plants possessed bipinnatifid fronds within an area of a few square yards. The herbarium material of this species shows that there is considerable variation in the degree of incision of the pinnae. Hence, it is deemed inadvisable to confer varietal rank upon this group with bipinnatifid fronds.

Juveniles of this species bearing simple, pinnatifid fronds or fronds bearing only a few pinnae bear little resemblance to the mature plants. *Lomaria decipiens* appears to have been founded on such juvenile plants.

The pink colour of unfurling fronds of some old plants is a striking feature of this species in the field.

There is considerable variation among the African, Mascarene and Australian plants referred to this species. A larger range of non-African material would have to be examined before any subspecies could be recognized with certainty.

Habitat

In both the winter and summer rainfall areas of South Africa, *B. attenuatum* is confined almost entirely to forest habitats, but may occur in scrub, marginal to forest, along stream banks. The species appears to tolerate very low light intensities, but has not been seen by the author in unshaded, dry localities. In deep shade in forest, it may be found in boulder crevices, but is most frequent in humus beside streams. In very sheltered forest habitats, epiphyllous lichens of the genus *Strigula* may often be found growing on the older fronds. Individuals of this species frequently produce fertile fronds. In the south-western Cape Province, *B. attenuatum* occurs between 500 and 2000 ft. altitude, but in Natal it may be found between 2000 and 6000 ft. altitude.

Although this species is entirely terrestrial in southern Africa, it is frequently epiphytic on forest trees and tree-ferns (*Cyathea* spp.) in tropical Africa.

Type locality

'In insula Mauritii': Mauritius; type collected by Groendal.

Distribution

Cape Province

Albany: Blockhouse Kloof, *D'Urban s.n.* (OXF) (bipinnatifid); Grahamstown, *Barker 964* (CTK), *Guthrie s.n.* (BOL), *Zeyher s.n.* (CTM); Howieson's Poort, *MacOwan 1863, 1865* (CTM). **Caledon**: Rivier Zonder Einde, *Barnard s.n.* (CTM). **Cape Peninsula**: Constantiaberg, *Pillans 2692* (Herb. Pillans); Devils Peak, *Wolley Dod 2371* (BOL, K), *Wolley Dod 2372* (BOL), *Zeyher s.n.* (BOL); Hout Bay, *Prior s.n.* (K); Table Mountain, *Compton s.n.* (CT), *Flanagan 2406* (PRE), *Moss 10344* (J), *Rawson s.n.* (CTM), *Rehmann 688* (BM), *Rehmann 1162* (BM), *Schelpe 1157, 1185* (NU), *Wasserfall 85* (CTK, PRE), *Wilms 3909* (BM, K). **Cathcart**: Hogsback, *Brueckner s.n.* (NU). **Engcobo**: Engcobo, *McLoughlin s.n.* (TRV). **George**: Wilderness, *Levyns 808* (CT). **Humansdorp**: Kruisfontein, *Buchanan 22* (NH) (bipinnatifid). **King Williams Town**: Perie, *D'Urban s.n.* (OXF), *Flanagan 23* (PRE), *Sim s.n.* (TRV), *Sim s.n.* (PRE) (bipinnatifid). **Knysna**: Knysna, *Rex 841* (TRV), *Trimen s.n.* (BM); 'Deepwalls', *Smellie s.n.* (J). **Paarl**: Paarlberg, *Drège s.n.* (BM, K, OXF). **Stockenstrom**: Katberg, *Holland s.n.* (CTK). **Stutterheim**: Stutterheim, *Acocks 9093* (PRE); Dohne, *Flanagan 2267* (PRE, CTM), *Galpin 2453* (PRE), *D'Urban s.n.* (OXF) (bipinnatifid). **Uitenhage**: Krakakamma, *Rawson s.n.* (CTM), *Zeyher s.n.* (CTM, K); Van Stadensberg, *Zeyher 529* (BM, CTM). **Umtata**: Bazya, *Baur 6* (K). **Worcester**: Worcester, *Cooper 1737* (BM).

Without locality: Kaffraria, *Cooper 1430* (BM), *Cooper 1931* (K).

NATAL

Bergville: Cathedral Peak Area, *Box 3353* (BM), *Schelpe 620* (NU); Natal National Park, *Cliver 477* (NH), *Doidge s.n.* (PRE), *Hutchinson 4528* (K), *Hutchinson, Forbes & Verdoorn 50* (NH, PRE), *Mogg 4250* (PRE), *Schelpe 1472* (NU). **Durban**: Amamzintoti, *McFarlane 28* (CTK). **Eshowe**: Eshowe, *Rogers 24470* (J). **Impendhle**: Giants Castle, *Symons 504* (TRV). **Lions River**: Howick, *Schlechter 6773* (K); Karkloof, *Rycroft 549* (NU). **Nkandhla**: Nkandhla, *Schelpe 1693* (NU); Qudeni, *Allsopp 740* (NU), *Clarkson 102* (NU), *Fisher 866* (NH, NU). **Polela**: Bulwer, *Allsopp 867* (NU), *Clarkson 203* (NU), *Henkel s.n.* (NU). **Umgeni**: Pietermaritzburg, *Fisher 661* (NH, NU), *Fisher 683* (NU), *Moss 3759* (J), *D. Smith 146* (NU); Zwartkop, *Sim s.n.* (BOL, PRE, TRV). **Umvoti**: Ahrens, *Fisher 941* (NU, NH), *Fisher 528* (NU). **Umzinto**: Dumisa, *Rudatis 862* (BM). **Vryheid**: Swartfolosi, *Acocks 12840* (PRE).

Without locality: *Bolton s.n.* (BM), *Buchanan 161* (K) (bipinnatifid).

ORANGE FREE STATE

Harrismith: Witzieshoek, *Flanagan 2130* (CTM, PRE).

TRANSVAAL

Barberton: Barberton, *Burtt Davy 327* (TRV), *Pott 5583* (TRV), *Thorncroft 12, 90* (PRE); Kaapsche Hoop, *V. Wager 72* (PRE); Nelspruit, *Bosman s.n.* (PRE). **Belfast**: Belfast, *Bottomley s.n.* (PRE), *Doidge s.n.* (PRE), *Leendertz 2773, 2782* (TRV). **Ermelo**: Ermelo, *Scheepers s.n.* (TRV). **Letaba**: Magoebas Kloof, *Schelpe 1621* (NU). **Lydenburg**: Mariepskop, *Scott 22* (PRE). **Pietersburg**: Haenertsburg, *Eastwood 10* (TRV); The Downs, *Junod 4063* (PRE, TRV), *Moss & Rogers 493* (J); Woodbush, *Schweickerdt s.n.* (PRE, TRV). **Pilgrims Rest**: Graskop, *Hardcastle 39* (PRE); Kavyns Pass, *Schelpe 1635* (NU); Macmac, *Schelpe 1668* (NU) (bipinnatifid). **Rustenburg**: Donkerhoek, *Rose Innes 216* (J); Magaliesberg, *Pegler 962* (BOL, PRE), *Sanderson s.n.* (K); Rustenburg, *Pott. s.n.* (TRV). **Sabie**: Tweefontein, *V. Wager 55* (PRE). **Witbank**: Klipfontein, *Mogg 12575* (PRE). **Zoutpansberg**: Piesangshoek, *Burchell s.n.* (NU).

SWAZILAND

Horo Forest, *V. Wager 118* (PRE).

SOUTHERN RHODESIA

Inyanga District, Pungwe, *Fries, Norlindh & Weimarck 3826* (LD). Inyanga, *Henkel s.n.* (CTK). Chimanimani Mountains, *Swynnerton 835a* (K). Umtali, *Darling s.n.* (TRV).

PORTUGUESE EAST AFRICA

Mozambique, Manica e Sofala, Manica, *Pedro & Pedrogão 6460, 6560* (BM).

NYASALAND

Mezent Malsa, *Whyte s.n.* (K). Namassi, *Cameron 1* (K). Shire Highlands, *J. Buchanan 11* (K). Mlanje District, Mlanje Mountain, Luchenya Plateau, *L. J. Brass. 16743* (K, NY). Zomba District, Zomba Plateau, *Brass 16172* (K, NY).

TANGANYIKA

Kilimanjaro, *Greenway 3195* (K). Mainland west of Zanzibar, *Last s.n.* (K). Mount Meru, *W. Leighton s.n.* (K). Ulugurus, Morogoro, Morningside, *Bruce 15* (BM).

KENYA

Aberdares, Tisso Forest, *Napier s.n.* (K). Aberdares, Theta River, *Gardner s.n.* (K).

UGANDA

Kigezi, *Eggeling E. 3252* (BM). Kigezi, Kayonza Forest, *Sangster S. 350* (BM). Ruwenzori, Wimi R., *Scott Elliot 7882* (K).

BELGIAN CONGO

Ruwenzori, Butagu, *Bequaert 3918* (BR).

CAMEROONS

Cameroons, *Preuss 876* (BM).

SÃO TOMÉ

São Tomé, *Exell 437* (BM).

FERNANDO PO

Fernando Po, *Mann s.n.* (K).

Blechnum attenuatum (Sw.) Mett. var. **Holstii** (Hieron.) comb.nov.

Blechnum polypodioides (Sw.) Kuhn var. *Holstii* Hieronymus, *Die Pflanzenwelt Ostafrikas*, C, 81.

Differs from the type in having shorter fronds which are up to 50 cm. long and 9 cm. broad which are often widely spaced on a creeping rhizome up to 2 cm. diameter, clothed in small paleae. Stipe 0·2 cm. diameter.

The sterile fronds of this variety bear a strong resemblance to those of juveniles of typical *B. attenuatum*. However, their maturity is expressed in the production of fertile fronds. The creeping, epiphytic or saxicolous rhizomes are less massive than in the typical form and possess considerably smaller scales. It is considered inadvisable to sink this variety until further information is available about any intermediate forms between this variety and typical *B. attenuatum*.

DISTRIBUTION

TANGANYIKA

Kyimbila District, Rungwe, *Stolz 867* (K). Usagara, Itumba, *North-Wood s.n.* (K). Ulugurus, Morogoro, Lupangaberg, *Schlieben 2985* (BM, BR). Usambara, Mbarama, *Holst 2479* (K) (Type coll.).

KENYA

Aberdares, Theta River, *Gardner s.n.* (K). Mount Kenya, Kathita Gorge, *Schelpe 2623* (BM).

BELGIAN CONGO

Parc National Albert, Sect. Mutrara, *De Wilde 262* (BR).

CAMEROONS

Cameroon Mountain, *Box 3607* (BM).

FERNANDO PO

Fernando Po, *Guinea 2152* (BM).

(4) **Blechnum ivohibense** C. Chr.

Blechnum ivohibense C. Chr., *Arch. de Bot.* (*Caen*), *2*, *Bull. mens.* 211 (1928); C. Chr., *Dansk. Bot. Arkiv*, **7**, 105 (1932). *Blechnum umbrosum* Peter, *Flora von Deutsch Ost Afrika*, *Fedde Rep. Beiheft*, **40**, 1, 82 (1929).

Rhizome erect, up to 10 cm. long, 1·8 cm. diameter, sparsely paleaceous; paleae, subulate, black, 0·3 cm. long, 0·005 cm. broad. **Stipe** pale brown, darker at the base, *minutely but densely papillose*, channelled, 9–25 cm. long. **Frond** pinnate: sterile frond erect, glabrous, membraneous, *dark green*, 15–39 cm. long, 3–7 cm. broad, lanceolate, hardly decrescent below; fertile frond lanceolate, 20–25 cm. long, 2·5–3·5 cm. broad, somewhat reduced below. **Rachis** pale brown, minutely papillose. **Pinnae**: sterile pinnae lanceolate, dark green, somewhat falcate, with irregularly reflexed crenulate margin, 2·0–4·8 cm. long, 0·6–1·2 cm. broad, base wholly adnate to the rachis, apex acute-acuminate, or rounded in the lowest pinnae only; fertile pinnae linear, up to

2·7 cm. long, 0·1 cm. broad, base adnate to the rachis, apex acuminate. **Sori** linear lomarioid, extending almost the whole length of the fertile pinna; indusium minute **Spores** brown, 48·9 × 36·6 μ, enclosed in a perispore.

Habitat

No information on the habitat of this species is available except that it is a forest species

Type locality

Mount Ivohibe, Madagascar.

Distribution

Tanganyika

West Usambara, Kisimba above Mazumbae, *Peter 16489* (BM, BR). Uluguru Mountains, Lupangaberg, *Schlieben 2959* (BM, BR).

Portuguese East Africa

Zambesia: Serra do Gúrmè, Marrequelo, Rio Namituè, *Mendonça 2162* (BM).

(5) **Blechnum tabulare** (Thunb.) Kuhn.

Blechnum tabulare (Thunb.) Kuhn., *Fil. Afr.*, 94 (1868); Christ, *Farnk. d. Erde*, 179 (1897); Engl. & Prantl, *Nat. Pfl.*, **1**, 4, 249 (1902); C. Chr., *Ind. Fil.*, 160 (1906); Sim, *Ferns S. Afr.*, ed. ii, 187, t. 83 (1915). *Pteris tabularis* Thunberg, *Prodr.*, 171 (1800); *Fl. Cap.*, 732 (1823). *Pteris osmundioides* Bory, *Voy.*, **2**, 194, t. 32 (1804). *Pteris palmaeformis* Thouars, *Fl. Trist. d'Ac.*, 30 (1804). *Onoclea Boryana* Sw., *Syn. Fil.*, 111 (1806); Schkh., *Kr. Gew.*, 98, t. 105 (1809). *Lomaria Boryana* (Sw.) Willd., *Sp. Pl.*, **5**, 292 (1810); Kunze, *Linnaea*, **10**, 505 (1836); *op. cit.* **13**, 152 (1839); Pappe & Rawson, *Syn. Fil. Afr. Austr.*, 27 (1858); Lowe, *Ferns*, **4**, 149, t. 62 (1872); Hook. & Bak., *Syn. Fil.*, ed. ii, 180 (1874); Sim, *Ferns S. Afr.*, ed. i, 123 (1892). *Lomaria magellanica* Desv., *Mag. d. Ges. Naturf. Fr. Berl.*, **5**, 330 (1811); Desv., *Mem. Linn. Soc. Par.*, **6**, 289 (1827); Hook., *Garden Ferns*, t. 52 (1862); Hook. fil., *Fl. Antarct.*, **2**, 393 (1847); Hook., *Sp. Fil.*, **3**, 27 (1860). *Lomaria coriacea* Schrad., *Gott. gel. Anz.*, 916 (1818). *Lomaria robusta* Carm., *Trans. Linn. Soc.*, **12**, 512 (1818). *Lomaria cinnamonea* Kaulf., *Enum. Fil.*, 154 (1824). *Lomaria setigera* Gaud., *Ann. Sci. nat.*, **5**, 98 (1825). *Blechnum Boryanum* (Sw.) Schlecht., *Adumb.*, 35, t. 19 (1827). *Lomaria palmaeformis* (Thouars) Desv., *Prod.*, 290 (1827). *Lomaria salicifolia* Kunze, *Linnaea*, **9**, 58 (1834); Fée, *Gen.*, 70 (1850–2). *Parablechnum salicifolium* (Kunze) Presl, *Epim. Bot.*, 110 (1849). *Lomaria Gueinzii* Moug.; Fée, *Gen.*, 69 (1850–2); Moore, *Ind.*, 197 (1860). *Lomaria robusta* Fée, *Gen.*, 69 (1850–2). *Lomaria spissa* Fée, *Gen.*, 71 (1850–2). *Blechnum magellanicum* (Desv.) Mett., *Fil. Lech.*, **1**, 14 (1856). *Lomaria cycadoides* Pappe & Rawson, *Syn. Fil. Afr. Austr.*, 28 (1858). *Blechnum Schottianum* Mett., *Ann. Sci. nat.*, **4**, 15, 71 (1861). *Lomaria Dalgairnsiae* Pappe & Rawson, *Syn. Fil. Afr. Austr.*, 27 (1858). *Blechnum salicifolium* (Kunze) Ettingsh., *Denkschr. Ak. Wien*, **23**, 63, t. 7, f. 8 (1864). *Blechnum cycadoides* (Pappe & Rawson) Kuhn, *Fil. Afr.*, 91 (1868); C. Chr., *Ind. Fil.*, 153 (1906). *Blechnum Dalgairnsiae* (Pappe & Rawson) Kuhn, *Fil. Afr.*, 92 (1868); C. Chr., *Ind. Fil.*, 153 (1906). *Lomaria tabularis* (Thunb.) Mett., Bak., *Fl. Brasil*, **1**, 2, 418 (1870). *Spicanta osmundioides* (Bory) O. Ktze., *Rev.*, **2**, 821 (1891).

Rhizome erect, frequently shortly arborescent, to procumbent, up to 90 cm. long, 9–30 cm. diameter, paleaceous; paleae, linear-lanceolate, 2–5 cm. long, 0·3–0·6 cm. broad, dark brown, sometimes spirally twisted. **Stipe** brown, channelled, paleaceous at the base, otherwise glabrous, 10–25 cm. long. **Frond** pinnate: sterile frond lanceolate, suberect to patent, glabrous above, more or less glabrous below when mature, *coriaceous*, 30–100 cm. long, 8–25 cm. broad, usually somewhat reduced towards the base, apex acute to acuminate; fertile frond erect, oblong-lanceolate, 30–100 cm. long, 5–20 cm. broad. **Rachis** brown, channelled, paleaceous when young, becoming glabrous with age. **Pinnae**: sterile pinnae lanceolate to oblong-lanceolate, *entire*, occasionally overlapping, 4–13 cm.

ong, 1·1–2·0 cm. broad, coriaceous, apex acute, *base unequally cuneate*, adnate to the achis; fertile pinnae linear, 5–12 cm. long, 0·4–0·6 cm. broad, sessile, set at an acute angle o the rachis, apex narrowly acute. **Sori** linear, lomarioid, extending almost the length f the fertile pinna; indusium brown, 0·2–0·3 cm. broad, entire, becoming torn at maturity. **pores** light brown, 55·8 × 34·8 μ, with a perispore.

In South Africa, the shape of the fronds and pinnae in this species varies widely accord-ng to the exposure of the habitat. Despite the plasticity shown by the African plants, it s possible that populations of *B. tabulare* in temperate South America, Tristan da Cunha, Madagascar and the Mascarene Islands may constitute recognizable subspecies. The author ias not been able to find satisfactory characters by which individuals from these isolated ireas could be distinguished.

Schkuhr (1809) published a plate (t. 105*b*) showing a fertile blechnaceous frond referred y him to *Onoclea Boryana*. The pinnae are long, linear with their bases adnate to the achis. In the text (p. 98), he refers to the specimen figured as having been placed 'unter smunda nov. sp. ohne Vaterland'. It appears to be a figure of a fertile frond of *B. attenuatum*.

A specimen annotated '*B. Dalgairnsiae*' in Rawson's Herbarium, now in the British Museum (Nat. Hist.), is undoubtedly *B. tabulare*. Its locality is given as Knysna, but there s no note which might have given Hooker (1862) reason to regard its habitat as 'dense orests of the Knysna'. Although the species is frequently seen in exposed habitats, it ery rarely survives in forest habitats.

HABITAT

B. tabulare is usually found in exposed situations, though it may occur less frequently n forest margins. In short grassland, it often grows about boulder bases, but may ccasionally form a recognizable community in depressions in grassland as it does on the ummit of the Pietermaritzburg Table Mountain. It also occurs frequently in small atches of open marsh grassland. Although this species appears to tolerate relatively igh light intensities it seems to require a fair amount of water in the substrate.

In the south-western Cape Province it occurs between 1000 and 3200 ft. altitude, while n Natal its altitude limits are approximately 2800 to 4300 ft. altitude. In tropical Africa, he species occurs between 6000 and 7000 ft. altitude.

TYPE LOCALITY

'In lateribus aquosis summi Taffelberg', i.e. on the summit of Table Mountain, Cape eninsula. The type specimen was collected by Thunberg, and is now at Uppsala.

DISTRIBUTION

APE PROVINCE

Caledon: Hottentots Holland, ravine, *Esterhuysen 4388* (BOL). **Cape Peninsula**: onstantiaberg, *Compton 8556* (CTK); Table Mountain, *Compton 10644* (CTK), *Humbert 638* (PRE), *Marloth 423* (PRE), *Moss 3763* (J), *Thode A. 67* (PRE), *Thunberg s.n.* (BM) Type coll.), *Wilms 3908* (BM), *Wolley Dod 1017* (BOL), *Zeyher s.n.* (BM). **Clanwilliam**: edarberg, Boskloof, *Pocock 139* (PRE). **George**: Cradockberg, *Burchell 5923, 5985* (K); eorge, *Burchell 5839* (K), *Fogg s.n.* (TRV); Montagu Pass, *Rehmann 93* (BM). **King Villiams Town**: Perie, *Sim, s.n.* (TRV). **Knysna**: Knysna, *Rawson s.n.* (BM), *Rex s.n.* TRV), *Trimen s.n.* (BM). **Mount Currie**: Kokstad, *Mogg 2005* (PRE). **Riversdale**: angeberg, *Muir 307* (PRE). **Swellendam**: Swellendam, *Holland s.n.* (CTK).

ATAL

Entonjaneni: Melmoth, *Mogg 4565* (PRE). **Ixopo**: Ixopo, *Schlechter 6649* (BM, TRV, K). **ions River**: Howick, *Hutton 139* (BM). **New Hanover**: Dalton, *Handley 97* (NU). **kandhla**: Nkandhla, *Schelpe 1703* (NU); Qudeni, *Allsopp 753* (NU), *Clarkson 77* NU), *Fisher 835* (NU, PRE). **Richmond**: Richmond, *Sanderson 101* (K). **Umgeni**:

Pietermaritzburg, *Fisher 545* (NU); Hilton Road, *Sim s.n.* (PRE). **Umvoti**: Greytow *Fisher 529* (NU), *Wilms 2403* (K). **Umzinto**: Dumisa, *Rudatis 1058* (BM, K).

Transvaal

Barberton: Barberton, *Thorncroft 56* (PRE); Mauchsberg, *Burtt Davy 485* (TRV Nelshoogte, *Schelpe 1673* (NU). **Lydenburg**: Mariepskop, *Scott 35* (PRE); Spitzkop *Wilms 1750* (BM). **Pietersburg**: Haenartsberg, *Pott 4666* (TRV); The Downs, *Junc 4043* (TRV). **Pilgrims Rest**: Erasmus Kop, *Hardcastle 38* (PRE); Gold Fields, *Ayre s.n.* (NH); Graskop, *Rogers 23044* (TRV); Kavyns Pass, *Munro s.n.* (*Moss 21157*) (J *Schelpe 1656* (NH, NU); Pilgrims Rest, *Moss 18848* (J); Sabie, *Cunliffe s.n.* (*Moss 376* (J). **Rustenburg**: Magaliesberg, *Sanderson s.n.* (K).

Swaziland

Horo Forest, *V. Wager 119* (PRE).

Southern Rhodesia

Darlington, *Bennett, 34, 42* (SAL). Chimanimani Mountains, *Swynnerton 835* (SAL Inyanga Down, *Fries, Norlindh & Weimarck 4687* (LD). Inyanga, Umtarazi Falls *Hopkins B. 1599* (SAL). Gazaland, Lusitu River, *Swynnerton 836* (K). Manica, Nuza *Gilliland 266, 498* (BM, J, SAL), *Gilliland 2059* (BM). Melsetter, Orange Kop, *Wild 195* (SAL). Makoni, *Eyles 3488* (SAL). Umtali, *Bennett 17a* (SAL), *Darling s.n.* (TRV *Holland s.n.* (CTK).

Northern Rhodesia

Mwinilunga District, Dobeka River, *Milne Redhead 3706* (K).

Portuguese East Africa

Chimanimani Mountains, Morebani, *Johnson s.n.* (K). Manica, Manica e Sofala, *Pedr & Pedrogão 6943, 7020* (BM).

Nyasaland

Kyimbila District, *Stolz 1111* (BM), *Stolz 656* (K). Luchenya Plateau, Mlanje Mountain *Brass 16480* (K, NY). North Nyika District, Nyika Plateau, *Brass 17210* (K, NY Zomba, *Mahon s.n.* (K).

Tanganyika

Kilimanjaro, *Schlieben 4693* (BM, BR). South Pare Mountains, *Peter 8837, 8865 12062* (K). Upper Ruhudje, Lupembe, Mpoponzi, *Schlieben 1068a* (BM); Lupembe *Schlieben 233, 725, 1068, 1170* (BR).

Uganda

Butale, near Kabale, *Synge 1214* (BM). Butale, Kigezi, *Thomas 2038* (K). Kigezi Lake Bunyoni, *Longfield 64* (BM).

Belgian Congo

Kabango, *Becquaert 6177* (BR). Kahusi, *Hendrickx 435* (BR). Kanzibi, Lac Kivu *Humbert 7519* (BR). South of Kundelungu Plateau, *Schmitz 1975* (BR). Luomyole *Hendrickx 5913* (BR). East of Nyagezi, *Boutakoff 71* (BR). Ruanda, Kigali, *Becquet 77* (BR). Ruanda, *Scaetta 437* (BR). Tschitshiangutu, *Scaetta 1438, 1444* (BR).

Angola

Benguela, Colupiango, rampart of Serra do Moco, *Gossweiler 12485* (BM). Distric Huilla, *Welwitsch 203* (BM). Lundo, Rio Luma, *Carisso & Mendonça 350* (BM).

(6) **Blechnum capense** (L.) Schlecht.

Blechnum capense (L.) Schlecht., *Adumb.*, 34, t. 18 (1825); Christ, *Farnk. d. Erde.*, 178 (1897); Engl. & Prantl, *Nat. Pfl.*, **1**, 4, 249 (1902); C. Chr., *Ind. Fil.*, 152 (1906); Sim, *Ferns S. Afr.*, ed. ii, 186, t. 82 (1915); Black, *Fl. S. Austr.*, 38 (1922). *Osmunda capensis* L., *Mantissa*, 306 (1771). *Osmunda procera* Forst., *Prod.*, 414 (1786). *Onoclea procera* (Forst.) Spreng., *Schrad. J.* 1799, **2**, 267 (1799). *Blechnum procerum* (Forst.) Sw., *Syn. Fil.*, 115 (1801); Labill., *Pl. Nov. Holl.*, **2**, 97, t. 247 (1806). *Asplenium procerum* (Forst.) Bernh., *Schrift. Akad. Erf.*, *1802*, 17, t. 1, f. 1 (1802). *Onoclea capensis* (L.) Swartz, *Syn. Fil.*, 111 (1806); Thunb., *Prodr.*, 171 (1800), *Fl. Cap.*, 731 (1823). *Lomaria capensis* (L.) Willd., *Sp. Pl.*, 291 (1810); Kunze, *Linnaea*, **10**, 505 (1836); Pappe & Rawson, *Syn. Fil. Afr. Austr.*, 27 (1858); F. Muell., *Fragm.*, **5**, 121 (1866); Lowe, *Ferns*, **4**, 145, t. 59, 60 (1872); Benth., *Fl. Austr.*, **7**, 737 (1878); Bailey, *Lith. Ferns Queensl.*, t. 86 (1892); Bailey, *Queensl. Fl.*, **6**, 1964 (1902). *Stegania procera* (Forst.) R.Br., *Prod.*, 153 (1810). *Stegania minor* R.Br., *Prod.*, **1**, 153 (1810). *Lomaria minor* (R.Br.) Spreng., *Syst. Veg.*, **4**, 65 (1827). *Lomaria procera* (Forst.) Spreng., *Syst. Veg.*, **4**, 65 (1827); Hook., *Sp. Fil.*, **3**, 22 (1860); Hook., *Garden Ferns*, t. 53 (1862), *N.Z. Fl.*, 366 (1864); Lowe, *Ferns*, **4**, 139, t. 40 (1872); Hook. & Bak., *Syn. Fil.*, 179 (pt.) (1874); Hook., *Ic. Pl.*, **5**, t. 427, 428 (1842); Sim, *Ferns S. Afr.*, ed. i, 122 (1892); Rodway, *Tasm. Fl.*, 283 (1903). *Lomaria Sellowiana* Pr., *Tent.*, 142 (1836). *Lomaria latifolia* Col., *Tasm. J.*, **2**, 175 (1844). *Parablechnum procerum* (Forst.) Presl., *Epim. Bot.*, 109 (1849). *Blechnopteris procera* Trev., *Atti. Ist. Veneto*, **2**, 2, 166 (1851). *Blechnum minus* Ettingsh., *Denkschr. Akad. Wien*, **23**, 63, t. 8, f. 5, 12 (1864). *Lomaria eximia* F. Muell., *Fragm.* **5**, 188 (1866). *Lomaria confusa* Fourn., *Ann. Sci. nat.*, v, **18**, 316 (1873). *Lomaria duplicata* Potts, *Trans. N.Z. Inst.*, **9**, 491 (1877). *Spicanta capensis* (L.) O. Ktze., *Rev.*, 821 (1891).

Rhizome, procumbent, up to 45 cm. long, 4–8 cm. diameter, paleaceous; paleae, lanceolate, 0·9–1·5 cm. long, 0·4–0·6 cm. broad, brown. **Stipe** brown, channelled, paleaceous, becoming glabrous with age, 15–45 cm. long. **Frond** pinnate: sterile frond oblong-lanceolate, erect to suberect, more or less glabrous at maturity, 25–90 cm. long, 10–25 cm. broad, not reduced below, firmly membraneous to thinly coriaceous; fertile frond lanceolate-oblong, erect to suberect, 20–80 cm. long, 10–30 cm. broad. **Rachis** channelled, paleaceous when young becoming glabrous with age. **Pinnae**: sterile pinnae oblong-lanceolate, often somewhat overlapping, 7–13 cm. long, 1·4–2·0 cm. broad, firmly membraneous to thinly coriaceous, *margin minutely serrate*, apex narrowly acute, base rounded to widely cuneate, *petiolate*; fertile pinnae linear, 8–14 cm. long, 0·3–0·5 cm. broad, sessile, set at an acute angle to the rachis, apex narrowly acute, base narrowly cuneate. **Sori** linear, lomarioid, extending almost the whole length of the fertile pinnae; ndusium, brown, 0·1–0·2 cm. broad, torn at maturity. **Spores** light brown, $57{\cdot}0 \times 41{\cdot}9\,\mu$, with a reticulate perispore.

Recently, Wakefield (1943) and Crookes (1949) have questioned the synonymity of B. *capense* and *B. procerum*. The author has examined some material of this species group from Australasia besides the African material. There is considerable graded variation within this group, but no constant characters have been found whereby a separation of egregates in this group could be effected satisfactorily. A decision as to whether or not he Australasian plants constitute a separate subspecies would depend upon the results of urther study.

HABITAT

In South Africa, *B. capense* usually occurs on stream banks in forest or scrub, although it s often found on fully exposed stream banks. Occasionally it grows on marshy ground under arying degrees of shade. Individuals of this species are more often found in a fertile condition in the south-western Cape Province than in the eastern parts of South Africa. In the outh-western region of the Cape Province the species may be found between 1000 and 500 ft. altitude; in Natal its altitude limits appear to be 2500 to 5300 ft. altitude.

TYPE LOCALITY

'Habitat inter montes Cap b. spei, inter montem tabularem et Diaboli', i.e. between Devils Peak and Table Mountain, Cape Peninsula. The type specimen, collected by Koenig is in the Linnaean Herbarium.

DISTRIBUTION

CAPE PROVINCE

Adelaide: Winterberg, *Paterson 3256* (BOL, PRE). **Albany**: Albany, *Zeyher s.n* (K); Grahamstown, *Bolton s.n.* (K), *Holland s.n.* (CTK); Howiesons Poort, *Glass 79* (CTM), *Rennie 226* (CT). **Caledon**: Mossel River, *Potts 1640* (CTM); Voëlgat, *Louwren* *s.n.* (PRE). **Cape Peninsula**: Cape Peninsula, *Masson s.n.* (BM), *Sieber 4* (BM); Constantia, *Wilms 3911* (BM, K); Devils Peak, *Rehmann 878* (BM); Table Mountain, *Compto* *s.n.* (CT), *Drege s.n.* (BM), *Rawson 1054* (CTM), *Schelpe 1171* (NU), *Thode A. 67* (NH) *Moss 3761, 10354* (J), *Wallich s.n.* (BM), *Zeyher s.n.* (BM). **George**: George, *Burchell 584* (K). **Humansdorp**: Assegaibosch, *Thode A. 2585* (K, NH, PRE). **King Williams Town** Perie, *Sim s.n.* (TRV). **Knysna**: Knysna, *Marloth 5718* (PRE), *Fries, Norlindh &* *Weimarck 1318* (LD), *Rex s.n.* (TRV), *Smellie s.n.* (*Moss 21665*) (J), *Trimen s.n.* (BM) **Lusikisiki**: Magwa Falls, *H. Wager s.n.* (PRE). **Oudtshoorn**: Swartberg, *Pocock 22* (PRE). **Riversdale**: Vetrivier, *Muir 350* (BOL). **Stellenbosch**: Jonkershoek, *Levyn* *s.n.* (CT); Paradise Gorge, *Garside 4* (K). **Uitenhage**: Van Stadens Berg, *Burchel* *4700* (K); Van Stadens River, *Browning s.n.* (*Bolus 1717*) (BOL).

NATAL

Bergville: Cathedral Peak Area, *Wilker 76* (NU). **Durban**: Amamzintoti, *MacFarlane 3* (CTK). **Inanda**: Inanda, *Wood s.n.* (*MacOwan 1877*) (CTM). **Nkandhla** Nkandhla Forest, *Schelpe 1702* (NU). **Umgeni**: Zwartkop, *Sim s.n.* (BOL, PRE, TRV) **Without locality**: *Buchanan 30* (K) (atypical), *Bolton s.n.* (BM) (atypical).

TRANSVAAL

Barberton: Barberton, *Thorncroft 64* (PRE). **Pietersburg**: The Downs, *Roger* *21945* (TRV); Woodbush, *Eastwood s.n.* (TRV). **Pilgrims Rest**: Gold Fields, *Ayres s.n* (NH); Graskop, *Hardcastle 25* (PRE); Macmac, *Schelpe 1670* (NU); Pilgrims Rest *Rogers 18673* (TRV); Vaal Hoek, *Hardcastle s.n.* (*Moss 21977*) (J). **Zoutpansberg** Piesanghoek, *Watson s.n.* (PRE).

SOUTHERN RHODESIA

Umtali, Chirinda forest, *Swynnerton 832* (fide Sim).

NYASALAND

Mount Milanji, *Whyte s.n.* (BM).

(7) Blechnum punctulatum Sw.

Blechnum punctulatum Swartz, *Schrad. J., 1800*, **2**, 74 (1801); Christ, *Frank. d. Erde* 178 (1897); Engl. & Prantl, *Nat. Pfl.*, **1**, 4, 249 (1902); C. Chr., *Ind. Fil.* 158 (1906) Sim, *Ferns S. Afr.*, ed. ii, 181, t. 78 (1915). *Lomaria auriculata* Desv., *Mag. d. Ges* *Naturf. Fr. Berl.*, **5**, 330 (1811). *Lomaria densa* Klf., *Enum. Fil.*, 151 (1824). *Lomari* *punctulata* (Sw.) Kunze, *Linnaea*, **10**, 505 (1836); Lowe, *Ferns*, **4**, 135, t. 53 (1872) Hook. & Bak., *Syn. Fil.*, ed. ii, 179 (1874); Sim, *Ferns S. Afr.*, ed. i, 118 (1892). *Mesothema punctulata* (Sw.) Pr., *Epim. Bot.*, 113 (1849). *Lomaria rigida* Fée, *Gen.*, 68 (1850–2) *Blechnopteris punctulata* (Sw.) Trev., *Atti Ist. Veneto*, **2**, 2, 166 (1851). *Lomaria Dregean* Fée, *Mem. 10*, 9 (1865). *Struthiopteris Dregeana* (Fée) Trev., *Atti Ist. Veneto*, **3**, 14, 57 (1869). *Struthiopteris punctulata* (Sw.) Trev., *Atti Ist. Veneto*, **3**, 14, 573 (1869). '*Lomari* *australis* L.', Lowe, *Ferns*, **4**, 143, t. 62, 63 (1872). *Spicanta punctulata* (Sw.) O. Ktze. *Rev.*, **2**, 822 (1891).

Rhizome procumbent to suberect, up to 30 cm. long, 2·5–4 cm. diameter, paleaceous; paleae, lanceolate-subulate, 0·5–1·8 cm. long, 0·1–0·2 cm. broad, dark brown. **Stipe** brown, darker below, channelled, glabrous, paleaceous at base, 3–15 cm. long. **Frond** pinnate: sterile frond lanceolate, erect, glabrous, coriaceous, 5–80 cm. long, 2–15 cm. broad, reduced below with the lowest pinnae deflexed; fertile frond lanceolate, erect, 5–60 cm. long, 2–18 cm. broad, reduced below. **Rachis** light brown, channelled, glabrous. **Pinnae**: sterile pinnae lanceolate, frequently slightly falcate, often more or less overlapping, glabrous, entire to minutely irregularly crenate, 3–7 cm. long, 0·6–1·3 cm. broad, subsessile, coriaceous, equally to unequally cordate or auricled at the base (upper lobe

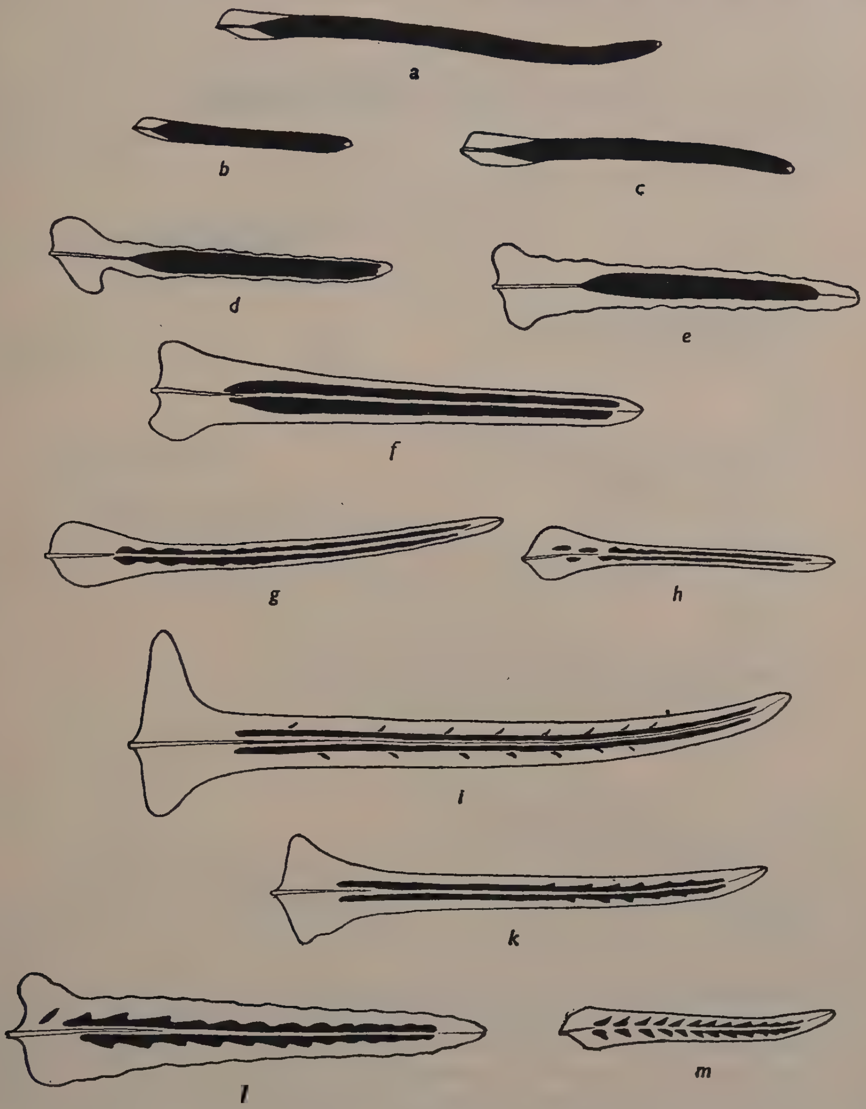

Fig. 1. **B. punctulatum** Sw. *a*, *D'Urban s.n.*, Kowie Road; *b*, xeromorph (× 2), *D'Urban s.n.*, Kowie Road; *c*, *D'Urban s.n.*, Cape Province. **B. punctulatum** var. **Atherstonei.** *d*, *McKen & Buchanan s.n.*, Natal; *e*, *Drege s.n.* (OXF); *f*, *Natal Herb.* 26679; *g*, *Natal Herb.* 26243; *h*, *Natal Herb.* 9703. **B. punctulatum** var. **intermedium.** *i*, *Fisher* 844; *k*, *Clarkson* 78; *l*, *William* 102; *m*, *Natal Herb.* 9700. Sori mature in *a–f* and in *l*; sori somewhat immature in *g–k*. (× 1.)

rarely adnate to the rachis), apex acute to rounded, not mucronate; fertile pinnae linear, 2–7 cm. long, 0·2–0·35 cm. broad, subsessile, base unequally cuneate with a more or less prominent upper lobe, apex widely acute. **Sori** linear, lomarioid, extending almost the length of the fertile pinnae; indusium, subentire, 0·1 cm. broad. **Spores** light brown, 40·8 × 24·8 μ, smooth, without a perispore.

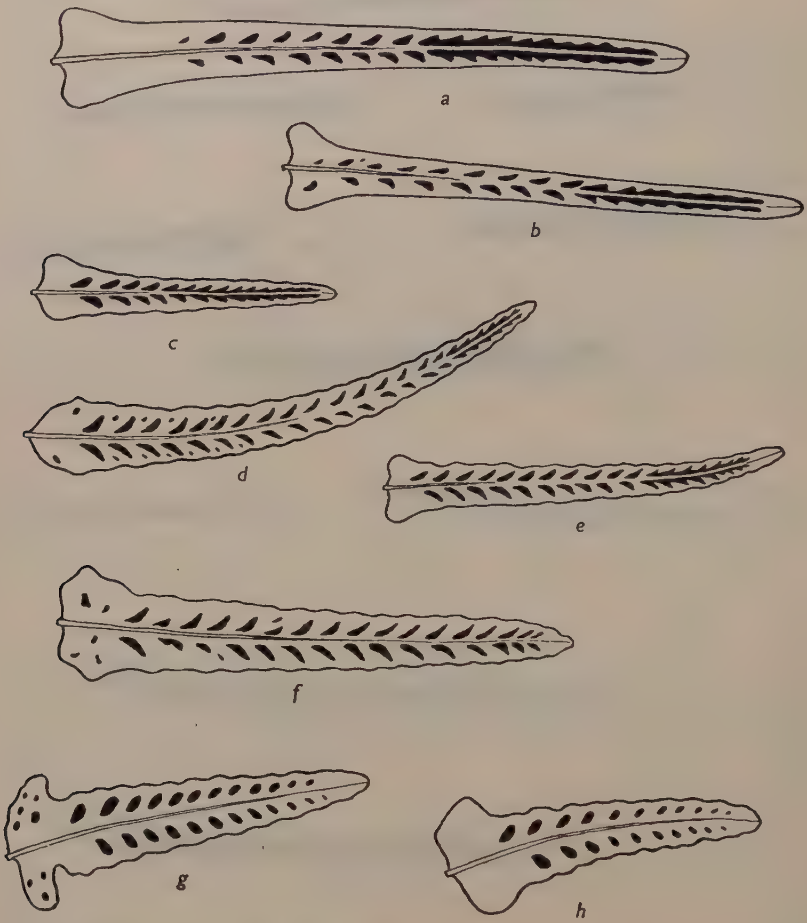

Fig. 2. **B. punctulatum** vars. (var. **intermedium**—var. **Krebsii** intermediates). *a, Natal Herb.* 25318; *b, Natal Herb.* 26687; *c, Natal Herb.* 26680; *d, Natal Herb.* 26681; *e, Natal Herb.* 26540. **B. punctulatum** var. **Krebsii.** *f, Natal Herb.* 26530; *g, Natal Herb.* 23644; *h, Natal Herb.* 26344. Sori mature in *g* and *h*; sori somewhat immature in *a–f*. (× 1.)

The taxonomic status of various individuals referred to *B. punctulatum* and its varieties has been the subject of some discussion. It is understandable that Kunze, and Pappe and Rawson, should have described the forms, regarded by Sim (1915) as *B. punctulatum* var. *Krebsii* and *B. punctulatum* var. *Atherstonei*, as species distinct from *B. punctulatum*, when one considers the relatively meagre material at their disposal. However, after examination of a wide range of material of this group, it is difficult to demarcate the limits of variation of the varieties recognized by Sim. The degree of disintegration of the longitudinal linear sori and the appearance of lateral sori constitute the characters on which the distinction between *B. punctulatum* and its varieties is based. These characters are extremely varied and intergrade. (Figs. 1, 2).

The fronds of individuals of the varieties of *B. punctulatum* exhibit progressive disintegration of the coenosori from the apex towards the base of the frond. Also, in some specimens, an increasing tendency towards a scolopendrioid soral pattern is shown in the same direction. Hence, only mid-frond pinnae are considered for purposes of comparison. The author examined a large population of *B. punctulatum* var. *Atherstonei* at the summit of Kavyns Pass, Transvaal, where all the fertile fronds seen exhibited closely similar soral patterns. It seems possible that some of these varieties are genetically distinct. The soral pattern of any one individual grown in culture does not appear to vary widely. The significantly larger spores of the variety *Atherstonei* may be regarded as indicative of a higher chromosome number as compared with the typical form. The difference in spore size between *B. punctulatum* and the variety *Krebsii* does not appear to be significant.

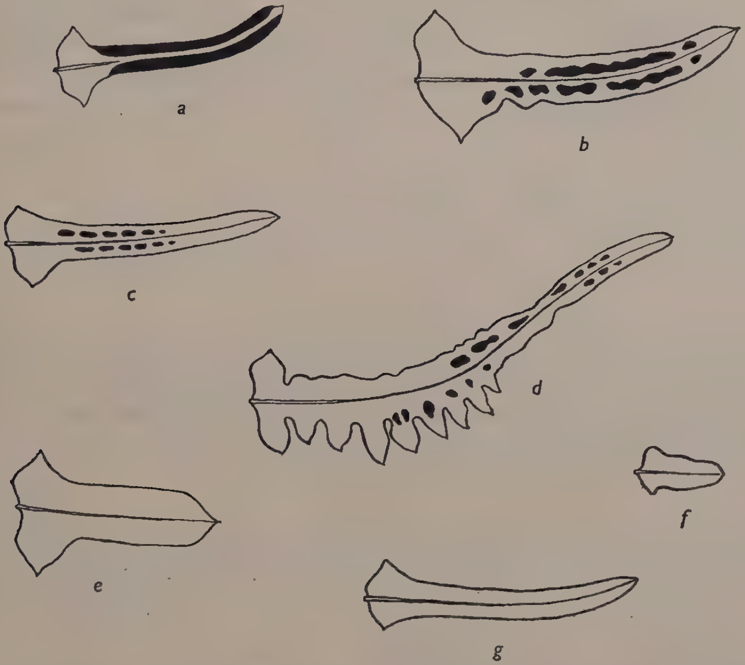

Fig. 3. **B. australe.** *a*, Typical fertile pinna (*D'Urban s.n.*, Perie); *b*, fertile pinna showing soral disintegration (*McCleland s.n.* Cape Peninsula); *c*, pinna with doodioid sori (*D'Urban s.n.*, Cape Province); *d*, bipinnatifid, partly fertile pinna (*D'Urban s.n.*, Cape Province); *e*, sterile pinna (*Schelpe*, P. 12); *f*, sterile pinna of a xeromorph (*Schelpe* 770); *g*, sterile pinna (*Allsopp* 835). (×1.)

The distribution areas of *B. punctulatum* and its varieties overlap (Fig. 4). Typical and xeromorphic *B. punctulatum* occurs commonly in the Cape south-western region in the winter rainfall area and also less frequently in the temperate parts of the summer rainfall eastern regions of South Africa. The varieties *Krebsii* and *intermedium* appear to be confined to the less temperate summer rainfall areas. Although the distribution of the variety *Atherstonei* overlaps that of these two varieties it extends much further northwards, possibly due to its apparent greater tolerance of dry conditions.

The varieties of *B. punctulatum* exhibit a wide range of soral patterns which intergrade between themselves and the typical form (Figs. 1, 2). Judging from the material available, ntermediates between the three varieties recognized by Sim (1915) and typical *B. punctulatum* appear to be less frequent than individuals which can be referred to *B. punctulatum* or its recognized varieties. Therefore, it is proposed that the varieties ecognized by Sim should be retained in view of taxonomic convenience.

Fronds with pinnatifid pinnae appear to be absent among *B. punctulatum* and it varieties. This character has been seen by the author in only one frond of *B. punctulatum* var. *Krebsii*, where the pinnatifid character was only slightly developed. Sim (1915 published a plate of a frond which he regarded as a bipinnatifid frond of *B. punctulatum* A specimen in the herbarium of the Transvaal Museum (TRV 277*c*), whose collection was examined by Sim, is extremely similar in outline to Sim's plate (ed. ii, t. 78). It was labelled '*B. punctulatum* bipinnate form' and appears to be the specimen figured by Sim The specimen has eublechnoid sori on the upper pinnae and has mucronate apices to the pinnae and to their basal auricular lobes. The specimen is therefore a bipinnate form of *B. australe* and not *B. punctulatum*. A number of bipinnatifid fronds of *B. australe* similar to Sim's figure, are known.

A small number of specimens which have more or less glandular fronds have been collected in widely separated localities ranging from the south-western Cape Province to Natal and Southern Rhodesia. Such glandular pubescence may occur on fronds varying from a normal size to extremely small xeromorphic fronds. The extent of this glandular pubescence varies greatly. The localities in which these specimens were collected indicate that these specimens are xeromorphs of *B. punctulatum*. These have been grouped under *B. punctulatum* f. *glanduliferum*.

At the other extreme, juveniles of this species growing in deep shade under humid conditions may form atypical sterile fronds with membraneous oblong pinnae with rounded serrate-crenate apices.

HABITAT

B. punctulatum usually occurs in forest, and occasionally in scrub marginal to forest. It is restricted to the more temperate regions of South Africa and is more frequent in the south-western Cape Province than it is in the eastern Transvaal or Natal. Infrequently, xeromorphs of this species may be found in exposed, dry rock crevices. In the south-western Cape Province it occurs between 300 and 2500 ft. altitude, but in Natal it may be found between 3000 and 5000 ft. altitude.

TYPE LOCALITY

'Prom. Bonae Spei', i.e. Cape Peninsula, Cape Province, collected by Thunberg.

DISTRIBUTION

CAPE PROVINCE

Albany: Grahamstown, *Sim s.n.* (TRV). **Bredasdorp**: Potberg, *Pillans 9452* (BOL). **Caledon**: Mossel Rivier, *Potts 1599* (CTM). **Cape Peninsula**: Hout Bay Nek, *Gamble 22239* (K); Lions Head, *Ecklon 29* (in part) (K); Llandudno, *Eyles 6466* (SAL); Simons Bay, *MacGillivray 377* (K); Table Mountain, *Alexander s.n.* (K), *Compton 10632* (CTK, PRE), *Gueinzius s.n.* (BM), *MacGillivray 378* (K), *Mitchell s.n.* (CT), *Rawson s.n.* (CTM), *Schelpe 1152, 1162* (NU), *Sieber 7* (BM), *Zeyher s.n.* (CTM); Tokay, *Wolley Dod 1284* (K); Cape Peninsula, *Gueinzius s.n.* (BM), *Masson s.n.* (BM). **Clanwilliam**: Olifants River Mountains, *Esterhuysen 15314* (BOL). **George**: George, *Schlechter 2465* (BM, K, TRV), *Trimen s.n.* (BM). **Humansdorp**: Assegaibosch, *Thode A. 2594* (K, NH, PRE). **Knysna**: Knysna, *Marloth 5709* (PRE), *J. Phillips s.n.* (*Moss 20930*) (J), *Rex s.n.* (TRV), *Smellie s.n.* (*Moss 21666*) (J). **Lusikisiki**: Umsikaba, *Drège s.n.* (BM). **Paarl**: Paarlberg, *Drège s.n.* (K). **Port Elizabeth**: Algoa Bay, *Cooper 2932* (K). **Riversdale**: Garcias Pass, *Muir 4581* (PRE). **Stellenbosch**: Jonkershoek, *Marloth 4924* (PRE); Paradise Gorge, *Garside 5* (K). **Swellendam**: Voormansbosch, *Sim coll.* (TRV). **Uitenhage**: Van Stadens Berg, *Ecklon & Zeyher 599* (in part) (K), *Zeyher 4617* (BM, CTM); Van Stadens River, *Browning s.n.* (BOL). **Umtata**: Bazya, *Baur 758* (K). **Umzimkulu**: Umzimkulu, *Drège s.n.* (fide Kunze). **Worcester**: Bains Kloof, *Kies 62* (CTK); Daljosaphat, *Tyson s.n.* (BOL). **Xalanga**: Cala, *Pegler 1633* (PRE).

NATAL

Inanda: Inanda, *Buchanan s.n.* (BOL, NH, TRV), *Wood s.n.* (NH). **Umzinto**: Dumisa, *Rudatis 972* (BM, K, PRE). **Umgeni**: Pietermaritzburg, Table Mountain, *Johnstone 69* (BM, NU).

Without locality: *Bolton s.n.* (BM), *Gerrard 498* (K), *Gueinzius s.n.* (K), *McKen 13* (K).

TRANSVAAL

Barberton: Barberton, *Thorncroft 16* (PRE). **Pilgrims Rest**: Erasmus Kop, *Hardcastle 18, 31* (PRE); Kavyns Pass, *Schelpe 1638* (NU). **Rustenburg**: Magaliesberg, *Sanderson s.n.* (K); Wolhuters Kop, *Bottomley s.n.* (PRE). **Zoutpansberg**: Entabeni, *Hutchinson & J. Gillet 4335* (K).

SOUTHERN RHODESIA

Victoria Falls, *Rogers 5546* (fide Sim).

TANGANYIKA

Ulugurus, Morogoro, Kinobe Road, *Bruce 111* (BM).

Blechnum punctulatum Sw. forma **glanduliferum** f.nov.

Differt a forma typica frondibus glandulosis nec glabris.

Differs from the type in having more or less glandular pubescent rachises and pinnae. Spores smooth, 40·8 × 27·6 μ.

TYPE LOCALITY

Cape Province, Uniondale Div., Konga Peak. *Esterhuysen 16252* (BOL).

The glandular character of the fronds is variable and is easily overlooked in herbarium specimens and in the field.

DISTRIBUTION

CAPE PROVINCE

Cape Peninsula: Devils Peak, *Molyneux s.n.* (BM); Table Mountain, Barrier Cave, *Schelpe 1871* (BOL). **Paarl**: Seven Sisters Mountain, *Esterhuysen 15809* (BOL). **Uniondale**: Kamanassie Mountains, Laudina, *Esterhuysen 16483* (BOL); Konga Peak, *Esterhuysen 16252* (BOL).

NATAL

Bergville: Drakensberg, Natal National Park, Mahai Valley, *Schelpe 1540* (BM, NU) (xeromorph).

BASUTOLAND

Leribe, *Dieterlen 72* (K)

SOUTHERN RHODESIA

Mazoe, Ironmask Hill, *Eyles 342* (BM).

Blechnum punctulatum Sw. var. **Atherstonei** (Pappe & Rawson) Sim.

Blechnum punctulatum Sw. var. *Atherstonei* (Pappe & Rawson) Sim, *Ferns. S. Afr.* ed. ii, 183, t. 79 (1915). *Lomaria punctulata* (Sw.) Kze. var. *Atherstonei* (Pappe & Rawson) Sim, *Ferns S. Afr.* ed. i, 120 (1892). *Blechnum Atherstonei* Pappe & Rawson, *Syn. Fil. Afr. Austr.* 16 (1858); Hook., *Sp. Fil.*, **3**, 31, 62 (1860).

Differs from the type in that the laminae of the fertile pinnae are much wider, 0·7–1·2 cm. broad, with the linear longitudinal sori interrupted in the basal pinnae and to a lesser extent in the mid-frond pinnae. Spores light brown, smooth, 54·1 × 33·9 μ, without a perispore.

Habitat

This variety is apparently confined in its distribution to forests and forest margins anc seems to tolerate a wide range of light intensities.

Distribution

Cape Province

Albany: Grahamstown (fide Sim). **Umtata**: Bazya, *Baur 460* (TRV).

Natal

Inanda: Noodsberg, *Buchanan s.n.* (NH), *McKen 13* (in part) (K), *Wood s.n.* (TRV) **Mapumulo**: Mapumulo, *Buchanan s.n.* (NH) **Nkandhla**: Qudeni, *Clarkson 78* (NU) *Fisher 844* (NU, PRE). **Umgeni**: Swartkop, *Clarkson 15* (NU), *Duncan Vale 21* (NU) **Umzinto**: Dumisa, *Rudatis 1682* (PRE).

Without locality: *Bolton s.n.* (BM), *Buchanan 155* (in part) (K).

Transvaal

Lydenburg: Mariepskop, *Scott 31* (PRE). **Pilgrims Rest**: Gold Fields, *Ayres s.n* (NH); Kavyns Pass, *Schelpe 1639, 1652* (NU); Vaal Hoek, *Hardcastle s.n.* (*Moss 21978*) (J).

Blechnum punctulatum Sw. var. **intermedium** Sim.

Blechnum punctulatum Sw. var. *intermedium* Sim, *Ferns S. Afr.* ed. ii, 184, t. 80 (1915).

Differs from the type in that the laminae of the fertile fronds are wider, 0·5–1·1 cm. broad, crenulate, with the soral segments set at an angle to the costa, giving a serrate outline at the base of the pinna, which grades into an undulate outline towards the apex of the pinna. Smaller soral segments frequently occur near the margin of the pinna besides those about the costa.

Habitat

This variety has been found growing among scrub, marginal to forest, and in open grassland. In shade in forest environments it appears to prefer drier situations.

Distribution

Cape Province

Albany: Amoskloof, *Holland s.n.* (CTK); Grahamstown, *Atherstone s.n.* (K), *Sim s.n.* (TRV). **Humansdorp**: Humansdorp, *Britten 1394* (PRE) (sterile). **Port St Johns**: Port St Johns, *B. Williams 102* (NU).

Locality unknown: Kaffraria, *Cooper 1429* (in part) (BM, K), *Cooper 2935* (K).

Natal

Inanda: Noodsberg, *Wood s.n.* (CTM). **Locality unknown**: *Buchanan 155* (in part) (K).

Blechnum punctulatum Sw. var. **Krebsii** (Kze.) Sim.

Blechnum punctulatum Sw. var. *Krebsii* (Kze.) Sim. *Ferns S. Afr.* ed. ii, 185, t. 81 (1915). *Lomaria punctulata* (Sw.) Kze. var. *Krebsii* (Kze.) Sim, *Ferns S. Afr.* ed. i, 122 (1892). *Lomaria Krebsii* (Kze.) J. Sm., *Hist. Fil.* 305 (1875). *Scolopendrium Krebsii* Kze., *Linnaea*, **18**, 118 (1844); Pappe & Rawson, *Syn. Fil. Afr. Austr.* 24 (1858). *Onychium Krebsii* Kze., *Linnaea*, **10**, 504 (1836).

Differs from the type in that the fertile pinnae are wider, 0·6–1·5 cm. broad, often irregularly crenate with a scolopendrioid soral pattern, with the sori arranged along lateral veins, adjacent pairs of sori facing in opposite directions. Such pairs of sori appear to form a single oval sorus at maturity. The sterile pinnae are less coriaceous than the sterile pinnae of the type, and frequently have larger basal auricular lobes. Spores, smooth, $45{\cdot}8 \times 30{\cdot}4\ \mu$, without a perispore.

Habitat

B. punctulatum var. *Krebsii* seems to be confined to moist shaded forest environments. It does not appear to have wide limits of tolerance towards humidity or light intensity.

TYPE LOCALITY

Near Grahamstown, Cape Province. The type is thought to be at Berlin, and not available at present.

DISTRIBUTION

CAPE PROVINCE

Albany: Grahamstown, *Atherstone s.n.* (K), *Burchell 3581* (K), *Glass s.n.* (CTM), *Guthrie s.n.* (BOL), *MacOwan 1863* (BM, CTM), *J. & B. Rennie 329* (CT), *Sim s.n.* (BOL). **Engcobo**: Engcobo, *McLoughlin 109* (TRV). **George**: George, *Rogers s.n.* (TRV).
Without locality: Kaffraria, *Cooper 1429* (in part) (BM, K).

NATAL

Durban: Amamzintoti, *MacFarlane 2* (CTK): Port Natal, *Guenzius s.n.* (K). **Inanda**: Inanda, *Buchanan s.n.* (BOL, NH), *Rehmann 8235* (BM), *Wood s.n.* (TRV); Verulam, *Wood s.n.* (CTM). **Lower Tugela**: Stanger, *Sim s.n.* (PRE). **Pinetown**: Kloof, *Clarkson 10* (NU), *Duncan Vale 13* (NU). **Umzinto**: Dumisa, *Rudatis 935* (BM, K, PRE).
Without locality: *Bolton s.n.* (BM), *Gerard 619* (K).

(8) Blechnum australe L.

Blechnum australe L., *Mantissa*, 130 (1767); Thunb., *Prodr.*, 172 (1800); Sw., *Syn. Fil.*, 114 (1801); Willd., *Sp. Pl.*, **5**, 410 (1810); Schkuhr, *Kr. Gew.*, **1**, 103, t. 110*b* (1809); Thunb., *Fl. Cap.*, 734 (1823); Schlecht., *Adumb.*, 38 (1825); Kaulf., *Linnaea*, **6**, 185 (1831); Mett., *Fil. Hort. Bot. Lips.*, 63, t. 3, f. 7 (1855); Hook., *Sp. Fil.*, **3**, 56 (1860); Hook. & Bak., *Syn. Fil.*, ed. ii, 186 (1874); Sim, *Ferns S. Afr.*, ed. i, 125 (1892); Christ, *Farnk. d. Erde*, 182 (1897); Engl. & Prantl, *Nat. Pfl.*, **1**, 4, 246 (1902); C. Chr., *Ind. Fil.*, 151 (1906); Sim, *Ferns S. Afr.*, ed. ii, t. 84 (1915). *Blechnum rigidum* Sw., *Schrad. J.*, *1800*, **2**, 75 (1801); *Syn. Fil.*, 114, 314 (1801); Willd., *Sp. Pl.*, **5**, 410 (1810); Hook., *Sp. Fil.*, **3**, 58 (1860). *Lomaria pumila* Kaulf. (non Raoul), *Enum. Fil.*, 151 (1824); Kunze, *Linnaea*, **10**, 508 (1836); Pappe & Rawson, *Syn. Fil. Afr. Austr.*, 29 (1858). *Lomaria minor* Link, *Hort. Berol.*, **2**, 80 (1833). *Lomaria australis* (L.) Link, *Fil. Hort. Berol.* 75 (1841). *Mesothema australe* (L.) Pr., *Epim. Bot.*, 111 (1849). *Mesothema rigidum* (Sw.) Pr., *Epim. Bot.*, 113 (1849). *Blechnopteris australis* (L.) Trev., *Atti Ist. Veneto*, **2**, 2, 166 (1851). *Struthiopteris australis* (L.) Trev., *Atti Ist. Veneto*, **3**, 14, 572 (1869). *Struthiopteris rigida* (Sw.) Trev., *Atti Ist. Veneto*, **3**, 14, 572 (1869). *Spicanta australis* (L.) O. Ktze., *Rev.*, 821 (1891). '*Blechnum punctulatum* Sw. bipinnate form', Sim, *Ferns S. Afr.*, ed. ii, t. 78 (1915).

Rhizome horizontal, *producing erect paleaceous crowns* at intervals, 1–3 cm. long, 1–2·5 cm. diameter, *on frondless* sparsely paleaceous, *slender rhizomes*, 15–50 cm. long, 0·2–0·4 cm. diameter; crown paleae, linear-lanceolate, 0·4–1·0 cm. long, 0·1–0·3 cm. broad, light to dark brown; rhizome paleae, ovate-lanceolate, 0·3 cm. long, 0·1 cm. broad, brown; the rhizome system in some xeromorphs may be reduced to a single procumbent crown. **Stipe** light brown, channelled, glabrous, paleaceous below, 4–20 cm. long. **Frond** pinnate; occasionally irregularly bipinnatifid; sterile frond oblong-lanceolate, erect to suberect, glabrous, firmly membraneous (coriaceous in xeromorphs), reduced below, 30–50 cm. long, 3·5–8·5 cm. broad (smaller in xeromorphs); fertile frond oblong-lanceolate, glabrous, firmly membraneous, 30–50 cm. long, 3·5–8·0 cm. broad (smaller in xeromorphs), reduced below. **Rachis** pale brown, channelled, glabrous. **Pinnae**: sterile pinnae lanceolate to oblong-lanceolate, often falcate, sessile, glabrous, entire or infrequently irregularly pinnatifid, 2–4 cm. long, 0·4–0·6 cm. broad, apex acute, *mucronate*, base auriculate, the *auricle lobes mucronate*, frequently overlapping; fertile pinnae linear-lanceolate, often strongly falcate, glabrous, entire, 2·0–4·3 cm. long, 0·2–0·4 cm. broad, apex acute, *mucronate*, base auriculate, auricles *mucronate*. **Sori** linear, occasionally interrupted on the lower pinnae, eublechnoid, extending almost the whole length of the fertile pinnae; indusium, entire, torn at maturity, 0·06 cm. broad. **Spores** light brown, smooth, 40·8 × 27·6 μ, without a perispore.

The mucronate apices of the pinnae and their basal lobes in *B. australe* constitute the most reliable vegetative character in its distinction from *B. punctulatum*. Xeromorphic plants of *B. australe* may exhibit little trace of apical mucrones and are consequently difficult to identify with certainty. However, if a few mucronate pinnae are present on the plant, the identity of such plants can be established as the pinnae of *B. punctulatum*, and their basal lobes are never mucronate. Occasionally, specimens of *B. australe* are seen in which the mucrones of the basal pinna lobes are more prominent than those of the apices of the pinnae themselves.

If fertile fronds are present, plants of *B. punctulatum* and *B. australe* can be distinguished on the character of the bases of the mid-frond pinnae. The bases of fertile pinnae of *B. punctulatum* are unequally cuneate with the upper lobe wider than the lower (Fig. 1).

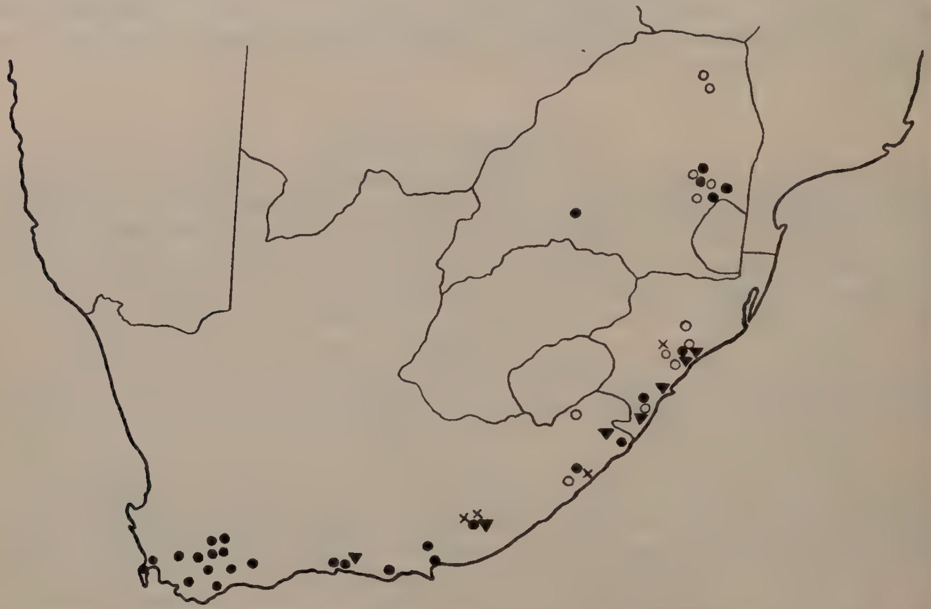

Fig. 4. Map of Southern Africa showing the distribution of *B. punctulatum* and its varieties. ●, *B. punctulatum*; ○, *B. punctulatum* var. *Atherstonei*; ×, *B. punctulatum* var. *intermedium*; ▼, *B. punctulatum* var. *Krebsii*.

The fertile pinna bases are equally cuneate or equally auriculate in *B. australe*. The long, slender rhizome of *B. australe*, which produces frond-bearing crowns at intervals, is characteristic of the species, except in extreme xeromorphs whose rhizomes are shorter and produce only single crowns at the apices of the rhizomes.

Plants of *B. australe* producing bipinnatifid fronds are infrequent and are possibly genetically distinct from the typical form. However, it appears that this character is only well developed under favourable environmental conditions and then only on the lower pinnae.

A number of glandular pubescent fronds closely resembling those of *B. australe* have been collected. Such individuals were referred by Sim (1915) to *B. auriculatum* Cav. The degree of pubescence is variable, and in some fresh specimens examined, pubescence was confined to small areas on the rachis about the pinna bases. Individuals in which this glandular character is well developed can easily be recognized in the field by the distinctly viscid fronds to which particles of dust adhere. The glandular hairs are less easily detectable on herbarium specimens, but are often best preserved about the bases of the pinnae.

Most of the glandular individuals have been found in rock crevices, and it is probable that this pubescence is a xeromorphic expression of a plastic species. A similar conclusion has been reached in the case of glandular individuals of *B. punctulatum*. In this revision, glandular individuals of *B. australe* are grouped under *B. australe* forma *glanduliferum*.

Partial disintegration of the sori to form a doodioid soral pattern may occur on fronds of *B. australe*, but this is usually confined to the lowest pinnae on otherwise typical fertile fronds. A few specimens have been found in which partial soral disintegration may occur up to the middle of the frond (Fig. 3). However, the degree of disintegration of these sori on the lower pinnae is extremely variable in such specimens.

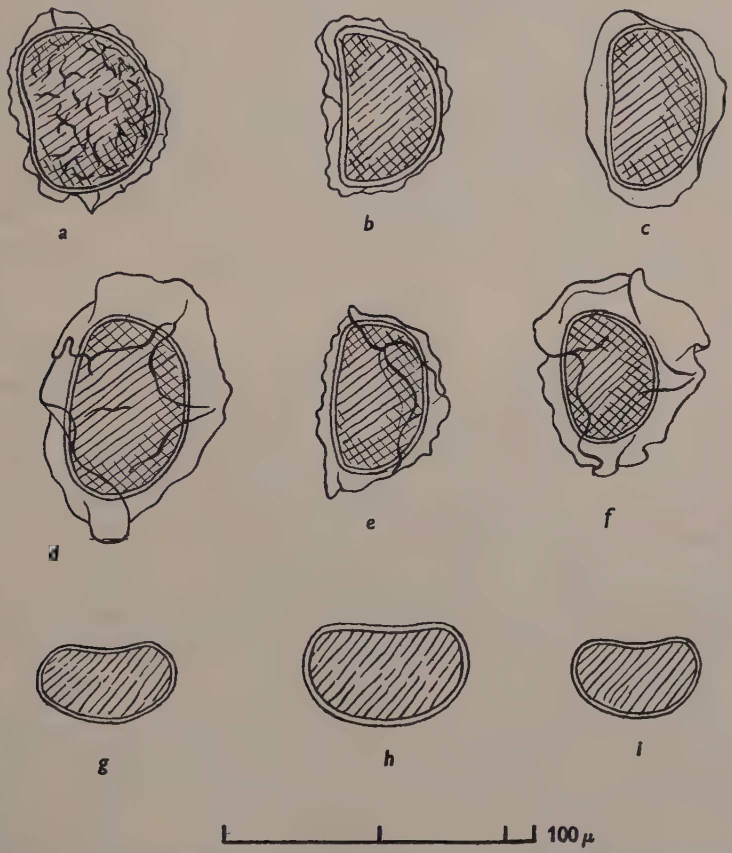

Fig. 5. Spores of African species of *Blechnum*. *a*, *B. capense*; *b*, *B. tabulare*; *c*, *B. attenuatum*; *d*, *B. inflexum*; *e*, *B. ivohibense*; *f*, *B. nudum* (from an Australian specimen); *g*, *B. punctulatum*; *h*, *B. punctulatum* var. *Atherstonei*; *i*, *B. australe*.

The taxonomic relation between the South African *B. australe* and the South American *B. australe* L., *B. auriculatum* Cav. and *B. hastatum* Klf. is still in question. The author has seen material of these three American *Blechna* in British herbaria, but considers the material inadequate to allow any definite conclusions on their relation to be reached. However, a few comments may be made. A number of South American specimens of this species group appear to be indistinguishable from the African *B. australe*. A number showed the frond-bearing crowns produced on slender rhizomes, characteristic of *B. australe*. Many of the specimens referred to *B. auriculatum* Cav. in herbaria, exhibit a much wider fertile lamina than is seen in African *B. australe*. In these South American specimens, the lamina on either side of the costa is not covered by the mature coenosori for up to a width of 0·1 cm. between the expanded sori and the costae. Often there is an uncovered marginal region of the lamina up to a width of 0·1 cm. In contrast, the lamina and often the costa is obscured by the expanded mature sori in the South African specimens. Also, many of the American specimens exhibit glandular pubescence to a varying degree.

HABITAT

B. australe is the most frequent species of the genus in South Africa. It appears to show wide tolerance towards light intensity and water supply, as it occurs on moist forest floors and in increasingly exposed and arid habitats to dry, sunny rock crevices. In the latter environment, compact xeromorphic forms, quite dissimilar to the type in general appearance, are produced. In the montane and midland forests of Natal and in some forests in the Cape Province, it often constitutes a noteworthy element of the forest floor vegetation. In more arid regions, such as in the mountains of the north-western Cape Province, it is almost confined to rock crevices. In East Africa it has been collected in forest at 6000 ft. altitude. The species occurs in the south-western Cape Province at altitudes between 1000 and 2500 ft. and in Natal between 2000 and 6000 ft. altitude.

TYPE LOCALITY

'Cap Bon. Spei', i.e. Cape Peninsula, South Africa. The type specimen is in the Linnaean Herbarium.

DISTRIBUTION

CAPE PROVINCE

Albany: Grahamstown, *Barker 547* (CTK), *Glass 599* (CTM); Howiesons Poort, *Rennie 330* (CT) (bipinnatifid). **Bedford**: Bedford, *Cook s.n.* (TRV). **Caledon**: Rivier Zonder Einde, *Barnard 408* (CTM). **Cape Peninsula**: Cape Peninsula, *Burchell 474* (K), *Harvey 312* (K), *Nelson s.n.* (BM), *Oldenburg s.n.* (BM), *Wallich s.n.* (BM, K); Constantiaberg, *Pillans 2693* (Herb. Pillans); Devils Peak, *Esterhuysen 15752* (BOL), *Wolley Dod 2373* (BOL); *Wilms 3907* (BM, K), *Zeyher 4618* (BOL); Kirstenbosch, *Clarkson 248* (BM, NU); Lions Head, *Ecklon 29* (in part) (BM); Steenberg Plateau, *Compton 3734* (BOL); Table Mountain, *L. Bolus s.n.* (CT), *Compton s.n.* (CT), *Drège s.n.* (CTM), *Garside 1434* (K), *Gamble 22163* (K), *Marloth 443* (PRE), *Moss 3760, 10342* (J), *Moss & Rogers 1710* (J), *Schelpe 1150, 1161, 1450* (NU), *Wilms 3907a* (K) (atypical), *Wolley Dod 2374* (BOL). **Ceres**: Elands Kloof, *Compton 16768* (CTK). **Engcobo**: Engcobo, *MacLoughlin 102* (TRV). **George**: George, *Schlechter 2478* (BM, K); Wilderness, *Levyns 807* (CT). **Graaff Rienet**: Graaff Rienet, *Bowker 35* (K). **Kentani**: Kentani, *Pegler 94* (PRE). **King Williams Town**: Perie, *Sim s.n.* (PRE) (atypical). **Knysna**: Knysna, *Michell s.n.* (BOL), *Trimen s.n.* (BM). **Komgha**: Kei Mouth, *Flanagan 183* (PRE, TRV). **Maclear**: Maclear, *Moss 18985* (J). **Molteno**: Broughton, *Flanagan 1684* (BOL, CTM); Looperberg, *Mogg 2669* (PRE). **Mount Currie**: Kokstad, *Mogg 1929* (PRE). **Paarl**: Paarlberg, *Drège s.n.* (BM, K). **Prince Albert**: Seven Weeks Poort, *Stokoe 1841* (PRE). **Queenstown**: Bongolo Nek, *Galpin 7975* (PRE). **Somerset East**: Boschberg, *MacOwan 259* (BM); Somerset East, *Bolus 327* (BOL) (bipinnatifid); Zuurberg, *Cooper 2930* (K). **Somerset West**: Somerset West, *Parker 4183* (CTK) (doodioid sori). **Stellenbosch**: Abdols Kloof, *Levyns s.n.* (CT); Jonkershoek, *Rycroft 604* (NU), *Schelpe 1868* (BOL), *Wasserfall 98* (CTK). **Stockenstrom**: Hogsback, *Young s.n.* (*Moss 17183*) (J). **Stutterheim**: Stutterheim, *Sister de Victoria s.n.* (PRE). **Uitenhage**: Van Stadens River, *Ecklon & Zeyher 599* (in part) (K); Zuurberg, *Fries, Norlindh & Weimarck 617* (LD). **Umtata**: Bazya, *Baur 214* (K). **Wellington**: Wellington, *Thompson s.n.* (PRE).

NATAL

Bergville: Drakensberg, Cathedral Peak Area, *Box 3368* (BM), *Schelpe 636, 749* (NU); Natal National Park, *Bottomley s.n.* (PRE), *Hutchinson, Forbes & Verdoorn 48* (NH, PRE), *Hutchinson 4526* (K); Oliviershoek Pass, *Schweickerdt 888* (TRV). **Lions River**: Karkloof, *Webb 136* (NU); Lidgetton, *Mogg s.n.* (PRE), *Roberts s.n.* (TRV). **New Hanover**:

Dalton, *Handley 101* (NU). **Polela**: Bulwer, *Allsopp 835* (NU), *Henkel s.n.* (NU); Centocow, *Thienel 53* (NU); Drakensberg Gardens Area, *Schelpe P.53* (NU); Underberg, *Webb 136* (NU). **Umgeni**: Boshoff Road, *Carnegie s.n.* (J); Hilton Road, *Sim s.n.* (BOL, PRE, TRV); Pietermaritzburg, *Tyson s.n.* (PRE). **Umvoti**: Ahrens, *Fisher 944* (NU); Greytown, *Sim s.n.* (TRV) (bipinnatifid, doodioid).

BASUTOLAND

Leribe, *Dieterlen 72* (in part) (CTM, NH, K). **Without locality**: *Cooper 766* (K).

ORANGE FREE STATE

Bethlehem: Clarence, *Van Hoepen s.n.* (TRV). **Ficksburg**: Ficksburg, *Cameron s.n.* (*Moss 16655*) (J).

TRANSVAAL

Barberton: Barberton, *Thorncroft 60* (PRE), *Wager 161* (PRE); Kaapsche Hoop, *H. Wager s.n.* (TRV). **Belfast**: Belfast, *Collins s.n.* (TRV), *Doidge s.n.* (PRE). **Ermelo**: Lake Chrissie, *Moss 17184* (J); Mavieriestad, *Pott 4845* (BOL, PRE, TRV), *Wilms 1744* (K). **Johannesburg**: Witpoortjie, *C. Moss 9791* (J). **Lydenburg**: Lydenburg, *Obermeyer 274* (TRV) (interrupted sori). **Middelburg**: Middelburg, *Jenkins s.n.* (TRV). **Pietersburg**: Haenartsburg, *Eastwood 16* (TRV); The Downs, *Junod 4031* (PRE, TRV). **Pilgrims Rest**: Pilgrims Rest, *Collins s.n.* (TRV), *V. Wager 182* (PRE). **Rustenburg**: Rustenburg, *Collins 98* (TRV), *Lanham s.n.* (TRV).

SOUTHERN RHODESIA

Melsetter, Lessop's Pass, *Fisher 1257* (BM, NU).

TANGANYIKA

Kibosho, *Daubenberger s.n.* (K, BR). Molo, Njoro, *Cholmley s.n.* (BM).

Blechnum australe forma **glanduliferum** f.nov.

Differt a forma typica frondibus glandulosis nec glabris.

'*Blechnum auriculatum* Cav.', Sim, *Ferns S. Afr.* ed. ii, 190, t. 76 (1915). '*Blechnum remotum* Pr.', Sim, *Ferns S. Afr.* ed. i (1892).

Differs from the type in that the fronds and rachises are more or less glandular pubescent. Spores, smooth, 45·0–48·3 × 31·2–34·8 μ, without a perispore.

TYPE LOCALITY

Cape Peninsula, Table Mountain, Barrier Ravine. *Schelpe 1870* (BM).

Specimens of this form do not appear to have the slender frondless rhizomes of the type, but these would be reduced or absent in xeromorphs. Sim (1915) gives an illustration of a fertile pinna of the plant which he refers to *B. auriculatum*, and describes the sorus as 'about halfway between the margin and the mid-vein, and with a distinct clear space between it and both'. The illustration and this description agree more closely with the South American material of *B. hastatum* than with the majority of South African glandular specimens closely similar to *B. australe*. Further collecting and culture experiments on the plants from the two localities quoted by Sim, will be required to elucidate whether Sim's plants were atypical ecological forms of *B. australe* or actually *B. hastatum*. None of the other collections cited under this form exhibits such distant sori.

DISTRIBUTION

CAPE PROVINCE

Cape Peninsula: Table Mountain, *Rawson s.n.* (TRV), *Schelpe 1780, 1782* (BOL). **Clanwilliam**: Cedarberg, *Schelpe 1922, 1926, 1948, 1977, 1985* (BOL). **King Williams Town**: Perie, *Flanagan 28* (PRE), *Sim s.n.* (NH, TRV). **Molteno**: Broughton, *Flanagan 1648* (PRE, TRV). **Namaqualand**: Khamiesberg, Beacon Hill, *Pearson 6373* (BOL, K). **Oudtshoorn**: Swartberg, *Schweickerdt s.n.* (PRU). **Uniondale**: Konga Peak, *Esterhuysen 16279* (BOL).

Natal

Bergville: Natal National Park, Mahai Valley, *Schelpe 2008* (NH). **Estcourt**: Giants Castle, *Symons 174* (TRV). **Nkandhla**: Nkandhla, *Schelpe 1700* (NH, NU).

Orange Free State

Witzieshoek, *Junod 10* (BR).

Acknowledgements

The author wishes to thank the Trustees of the British Museum (Nat. Hist.), London; the Director of the Royal Botanic Gardens, Kew; M. le Directeur, Jardin Botanique de l'Etat, Bruxelles; the Chief of the Division of Botany and Plant Pathology, Pretoria; the Curator of the Bolus Herbarium, University of Cape Town; the Directors of the Transvaal Museum and the South African Museum, the Director of the National Botanic Gardens, Kirstenbosch, and the curators of other herbaria who have given the author facilities for work. The author gratefully acknowledges valuable discussion and advice from Mr A. H. G. Alston and Mr F. Ballard.

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Herbarium abbrevations

Lanjouw (1939) has been followed in the choice of abbreviations for herbaria:

BM	British Museum (Nat. Hist.), London
BOL	Bolus Herbarium, Cape Town
BR	Jardin Botanique de l'Etat, Bruxelles
CT	Department of Botany, University of Cape Town
CTK	National Botanic Gardens, Kirstenbosch
CTM	South African Museum, Cape Town
J	Botany Department, Witwatersrand University, Johannesburg
K	Royal Botanic Gardens, Kew
LD	Botaniska Museet, Lund
NH	Natal Herbarium, Durban
NU	Botany Department, University of Natal, Pietermaritzburg
NY	New York Botanic Garden, New York, U.S.A.
OXF	Fielding Herbarium, Oxford
PRE	National Herbarium, Pretoria
PRU	Botany Department, University of Pretoria
SAL	Queen Victoria Memorial Museum, Salisbury, Southern Rhodesia
TRV	Transvaal Museum, Pretoria

An investigation into the stem apex of Syringa vulgaris L. with special reference to the formation of the leaf and leaf procambium. By J. G. VAUGHAN, Chelsea Polytechnic.

(With Plates **24** and **25**)

[Read 18 January 1951.]

INTRODUCTION

Philipson (1949) has recently reviewed the ideas of plant morphologists on the arrangement of cells in the stem apex. He explains, in some detail, the tunica-corpus concept. According to this concept the stem apex consists of two regions—an outer tunica and an inner corpus. The two regions differ according to the direction of cell divisions. In the tunica, cell divisions take place at right angles to the surface, while in the corpus, cell divisions take place in a number of directions. Sifton (1944), in a review of stem apex morphology, shows how the depth of the tunica varies—in *Triticum* and *Avena* it is one layer deep; in *Carya*, *Rhododendron* and *Morus* two; in *Artemisia* three, while in *Viburnum* it is four. Reeve (1948), however, calls for care in regarding the tunica-corpus concept as a fixed one, and claims to have demonstrated fluctuations in the depth of the tunica of a number of plants, particularly *Salix*. Nevertheless, this concept is well established in modern studies of stem apices. Philipson (1949) also writes of another interpretation of the stem apex—an interpretation based on cell size and density of protoplasmic contents. According to this the stem apex consists of a central zone of lightly staining cells and a peripheral zone of smaller, more darkly staining cells, the flank meristem. There is also a 'file meristem' which gives rise to the pith. Among others Majumdar (1942) supports this concept.

The position of initiation of the leaf seems to vary among the various genera that have been studied. Engard (1944) reviews this subject and states that, in most plants studied, the leaf appears to originate in the second and third layers of the apex. Louis (1935) made a valuable contribution to stem apex morphology when he introduced the conception of the 'foliar foundation' or 'foliar buttress', the meristematic base on which the leaf develops and which later forms part of the axis. Majumdar (1942) has supported this idea.

Perhaps one of the most interesting problems bearing on the study of the stem apex is the development of the tissue which gives rise to the vascular supply of the leaf, the so-called leaf procambium or leaf provascular meristem. This tissue is usually distinguished from surrounding tissues by the fact that it consists of elongated cells, the contents of which stain deeply. Quite a common belief is that the procambium originates at the base of a leaf primordium and then develops acropetally into the growing leaf and basipetally into the axis of the stem to join the general vascular system of the plant. Sifton (1944) summarizes the views of some workers who have supported this idea. They are Flot (1905, 1906, 1907), Herrig (1915), Bugnon (1921), Lange (1927), Langdon (1927), Yarbrough (1934), Foster (1935), and Cross (1936, 1937). In more recent years many workers have claimed to have demonstrated the continuity of procambium at all times, that is, the procambium supply of a particular leaf is continuous with the general vascular supply of the plant from the moment of initiation of the leaf. These investigators include Priestley, Scott & Gillett (1935), Boke (1941), Esau (1942), Majumdar (1942), Reeve (1942, 1948), Engard (1944), Lawalrée (1948) and Garrison (1949). Bearing this very recent work in mind, it is therefore surprising to find that Ball (1949) supports the oldish conception of leaf procambium developing acropetally and basipetally. Louis (1935) introduced the term 'prodesmogen' for tissue that gave rise to typical procambium. It was itself identical in constitution with the apical meristem and was defined by vacuolation and enlargement of surrounding cells. Helm (1931) and Kaplan (1937) held similar ideas. Later workers, however (Esau, 1942; Engard, 1944), have not been able to establish the existence of prodesmogen in the plants they have studied. After its initiation the leaf develops into a tiny protuberance, the primordium, on the surface of the apex. For a very short time the primordium consists entirely of meristematic cells with dense protoplasmic contents. However, the cells of the primordium soon undergo vacuolation and enlargement. It is during this process that the leaf procambium becomes most apparent. Vacuolation appears to start in the abaxial half of the leaf primordium and is followed by vacuolation in the adaxial half (Majumdar, 1942; Reeve, 1942; Engard, 1944; Miller & Wetmore, 1946; Philipson, 1947). During its early history the leaf primordium has a well-marked apical meristem (Reeve, 1942; Engard, 1944; Boke, 1947).

Material and methods

Syringa vulgaris L. was used for this investigation because it could be obtained easily and its opposite leaves were favourable for sectioning.

Vegetative buds were collected at regular intervals over the period October 1948–August 1949. They were collected from one tree in Ravenscourt Park and fixed on the spot in formalin acetic alcohol.

The results about to be described are based on observations made on sections of buds fixed in May 1949. The buds were embedded in paraffin wax and serial sections were cut at thicknesses of 6, 8 and 10μ. Observations were made mainly on sections 8μ thick. Both longitudinal and transverse sections were prepared. Longitudinal sections were found to be the more useful. This investigation involved the sectioning of about 200 buds.

Various combinations of stains were employed, and Heidenhain's iron haematoxylin alone was most satisfactory.

Photographs were taken through a $\frac{1}{6}$ in. parachromatic objective with a Leitz 'Mikam' eyepiece camera. Slow process plates were employed.

An account of the observations which have been made on *Syringa* can be given in a convenient form by the following description and figures. These figures have been made from a selected series of preparations which provide a clear demonstration of the point of view adopted in this paper.

Pl. **24**, fig. 1, represents a median longitudinal section 8μ thick through the stem apex of *Syringa*. The bases of two leaf primordia are shown, the left containing procambium. The apex is almost flat and is approximately 100μ wide. Using the tunica-corpus concept there appears to be one layer of cells in the tunica and approximately five layers of cells in the corpus. Cell divisions in the tunica are anticlinal, while those in the corpus are periclinal and in other planes. The tunica sometimes seems to consist of two layers of cells, but periclinal divisions in the second layer are fairly frequent. Considering the apex from the point of view of the size of the cells and the density of the cell contents, there is a well-marked central zone and a flank meristem of smaller more darkly staining cells. A file meristem, with cells in vertical rows, giving rise to the pith is clearly present. Between the central zone and the file meristem there is an intermediate zone of very much flattened cells. The depth of the apex from the surface to the intermediate zone is about 60μ.

Pl. **24**, fig. 2, represents a longitudinal section 8μ thick through a stem apex. The section is slightly oblique. Only part of the apex is shown. The important feature is the presence of a very small leaf primordium. It is clear that there has been much meristematic activity in the flank meristem. The small leaf primordium seems to have been raised by cell divisions, in various planes, in the two layers of cells underneath the tunica. The tunica, covering the primordium, still only undergoes divisions at right angles to the surface. Underneath the primordium there is to be seen the foliar foundation. There is a well-defined procambium strand supplying the foliar foundation and the leaf primordium. This strand is continuous with the general vascular supply of the bud and, as one may regard this condition as about the earliest stage in the development of the leaf primordium, it would seem that the procambial supply is continuous at all times. An oblique section such as this is usually more useful for tracing the vascular supply of a bud than a truly median one (see below). The procambium has been produced by longitudinal divisions in the inner part of the flank meristem. It is difficult to determine the exact point where the procambium strand stops in the apex. As one follows the strand up into the apical meristem the procambium cells become shorter, and in the uppermost levels of the strand the protoplasmic density of these cells is the same as that of the ordinary apical meristem cells. To illustrate this point, at level *A–B*, procambium cells can be seen running between ordinary apical meristem cells. Farther down the strand the procambium cells contrast strongly with the pith and cortical cells as the result of their dense protoplasmic contents and elongated nature—level *C–D*.

Pl. **25**, fig. 3, represents a median longitudinal section 8μ thick of a leaf primordium a little older than the previous one. The primordium is approximately 135μ high, and the section shows it curved over the apex. The tissue of this primordium can be regarded as being entirely meristematic, although the density of cell contents varies throughout the organ. There is a well-marked meristem at the tip of this primordium. The density of the protoplasmic contents of the cells that constitute this primordium apical meristem is the same as that of the cells that constitute the stem apical meristem. Procambium tissue is to be seen in the primordium, although it is not continuous in this particular section with the rest of the vascular system of the bud. However, a connexion can be established in a section further along the series. This apparent break in the continuity of the procambium is due to the fact that the strand runs obliquely into the leaf and, consequently, a truly median longitudinal section would show no continuity. Tangential longitudinal sections demonstrate that the procambium strand runs obliquely. The cells that make up the procambium have the usual elongated shape, and their contents stain just as deeply as those of the cells that make up the two apical meristems already mentioned. There is a connexion between the procambium and the leaf apical meristem, so it can be assumed that this meristem is responsible for producing new procambium as the leaf grows. The cells of the adaxial and abaxial tissues of the primordium have quite dense contents, although the density is not that of the two apical meristems and the procambium already mentioned. Like the procambium both adaxial and abaxial tissues, at this stage, are derived from the apical meristem of the primordium. The tunica is still to be seen covering the primordium, its dense cells undergoing anticlinal divisions. There is an indication of vacuolation in the abaxial tissue of what must be regarded as the foliar foundation. In the section there is to be seen a primordium of an axillary bud.

Pl. **25**, fig. 4, represents an oblique longitudinal section 8μ thick through a still older primordium. It is still curved over the stem apex and is approximately 156μ high. Procambium tissue is to be seen in the primordium. Continuity of this tissue with the rest of the vascular tissue of the bud is also obvious, the section being off the median plane. The cells that make up the surface layer of the primordium have dense protoplasmic contents, so that they can be assumed to be meristematic, undergoing divisions in the anticlinal plane. All these cells have originated from tunica of the stem apex. The tissues of the primordium have now undergone quite considerable vacuolation, this vacuolation having extended farther up the abaxial side of the primordium than the adaxial side.

A median longitudinal section through a somewhat later stage showed the leaf primordium standing nearly upright and about 240μ tall. Its apical meristem which was responsible for the growth in length of the primordium was still clearly visible. The procambium was present, but its continuity could not be demonstrated because the section was median. The cells of the primordium showed extensive vacuolation. The cells of the covering layer of the primordium, the primordial apical meristem and the procambium still had dense contents, but the rest of its tissues were quite highly vacuolated although mitotic divisions were still to be observed.

The observations described above were confirmed in transverse sections.

CONCLUSION AND DISCUSSION

Nearly 200 buds of *Syringa vulgaris* L. have been sectioned, and examination of these sections has shown that the stem apex of this plant can be divided, according to the direction of cell divisions, into two regions—an outer tunica and an inner corpus. The tunica consists of one layer of cells showing anticlinal divisions while the corpus consists of about five layers of cells showing periclinal divisions. Esau (1942) reports a similar condition in *Linum*. On the basis of cell size and density of cell contents the stem apex of *Syringa* shows the central zone, flank meristem and file meristem reported by various workers for other plants (Majumdar, 1942; Philipson, 1947).

Leaf initiation appears to take place in the outermost two layers of the corpus which, according to Engard (1944), is the most common position in the various plants that have been studied. When extremely young leaf primordia are examined, procambium is always to be found in close proximity. This procambium is produced by longitudinal divisions in the inner region of the corpus. There is no evidence at all to support the existence of the prodesmogen tissue of Louis (1935). Examination of numerous series of sections never reveals a break in the procambial network, and it therefore follows that the vascular system of the stem and leaf is continuous at all times. The leaf primordium develops on the foliar foundation with the procambium strand following into it. This gives very strong support to the work of such morphologists as Priestley *et al.* (1935), Boke (1941), Esau (1942), Majumdar (1942), Reeve (1942, 1948), Engard (1944), Lawalrée (1948) and Garrison (1949); and is in opposition to the work of Flot (1905, 1906, 1907), Herrig (1915), Bugnon (1921), Lange (1927), Langdon (1927), Yarbrough (1934), Foster (1935), Cross (1936, 1937) and Ball (1949).

It has been noted in the introduction that a number of workers have described the progress of vacuolation in the developing leaf, and that others have shown that the young leaf grows in length by the activity of an apical meristem. The work on *Syringa* now described is in full agreement with these other investigations.

SUMMARY

1. The stem apex of *Syringa vulgaris* L. has been examined.
2. The apex can be divided into a tunica and a corpus.
3. Under another scheme of classification the apex can be divided into a central zone, a flank meristem and a file meristem.
4. Leaves are initiated in the outer layers of the corpus.
5. Procambium is produced by longitudinal divisions of cells in the inner layers of the corpus.
6. The procambium supply of a leaf primordium is continuous at all times.
7. Vacuolation of the leaf primordium tissues is first abaxial and then adaxial.
8. The leaf primordium possesses an apical meristem.

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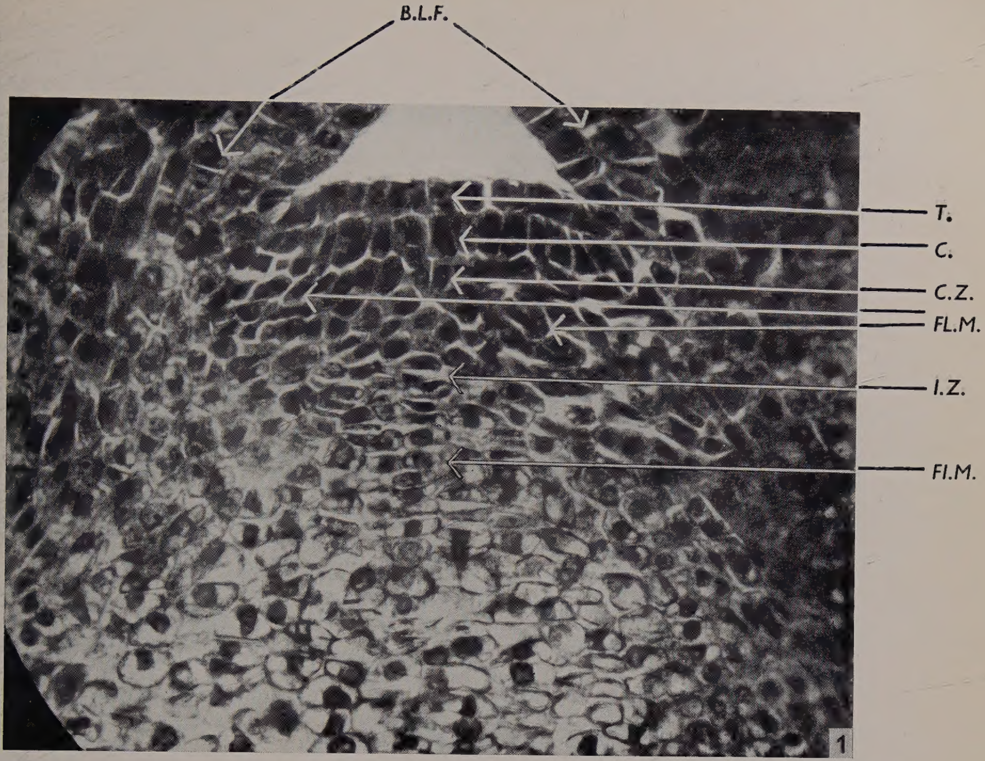
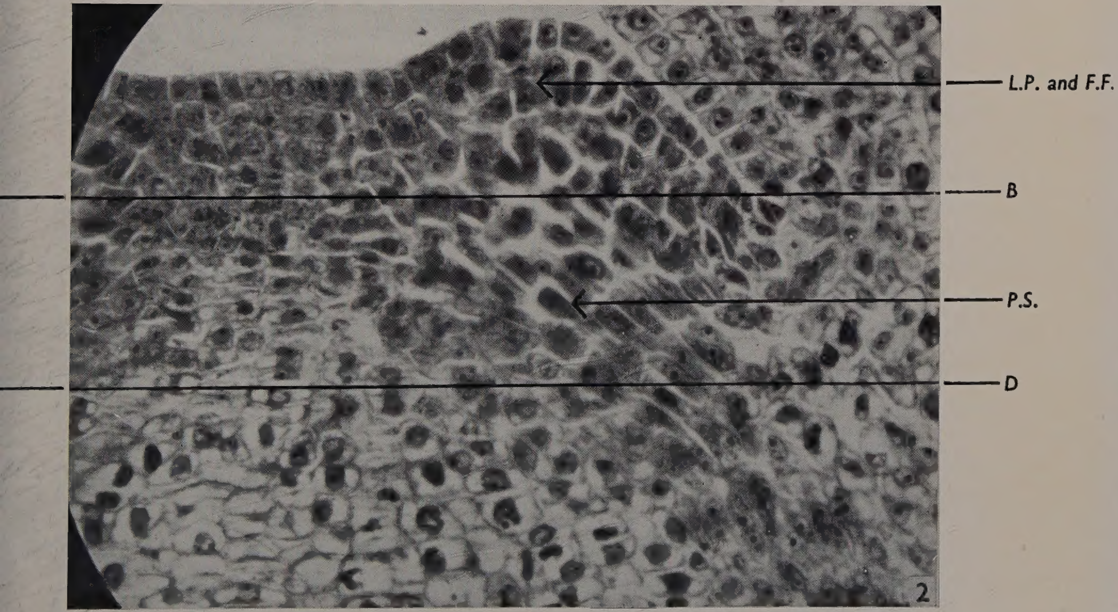
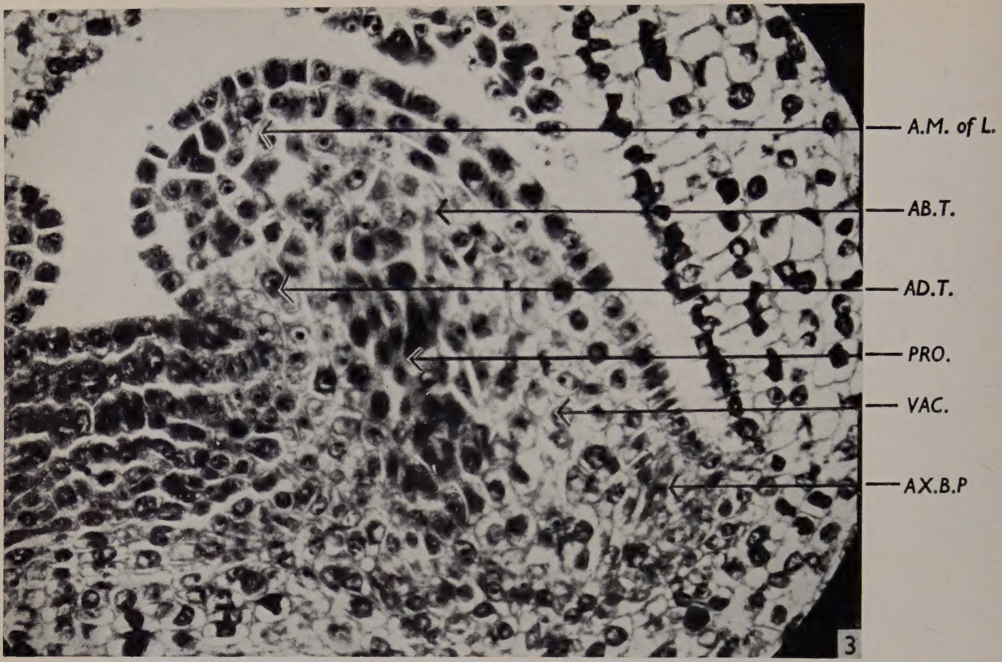
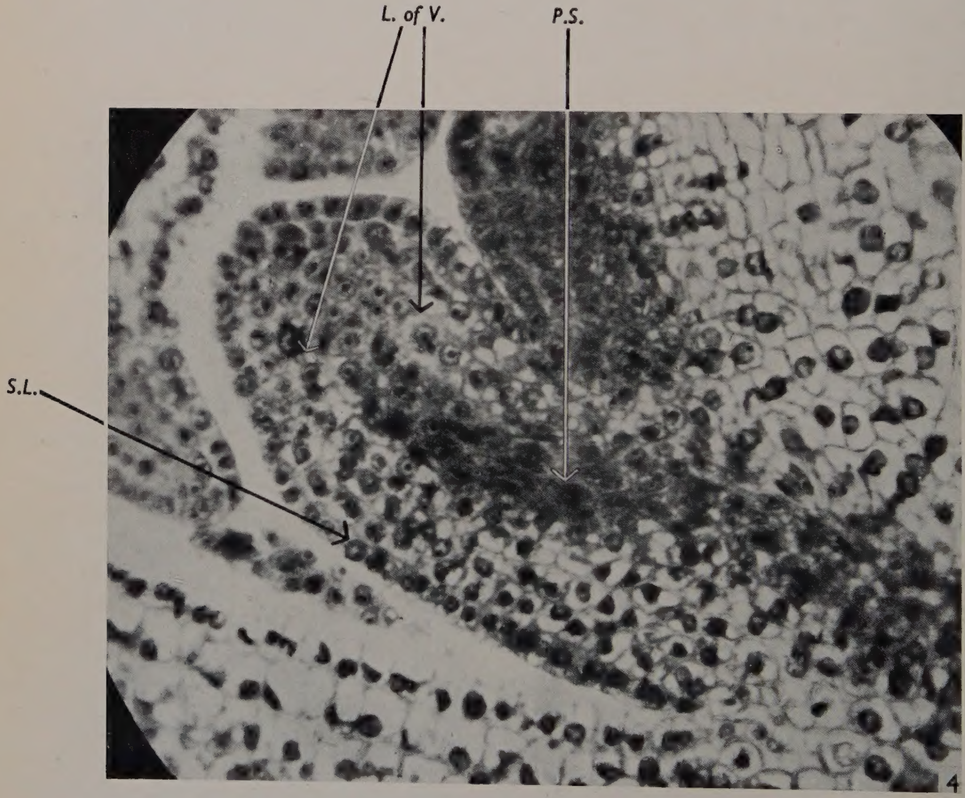




Stem apex of *Syringa*





Stem apex of *Syringa*

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EXPLANATION OF PLATES 24 AND 25

(All photographs from untouched negatives.)

Plate 24

Fig. 1. Photograph (×336) of a median longitudinal section, 8μ thick, of stem tip of *Syringa*. *B.L.F.*, bases of leaf primordia; *T.*, tunica; *C.*, corpus; *C.Z.*, central zone; *FL.M.*, flank meristem; *FI.M.*, file meristem; *I.Z.*, intermediate zone.

Fig. 2. Photograph (×336) of an oblique longitudinal section showing very young leaf primordium. *L.P.* and *F.F.*, leaf primordium and foliar foundation; *P.S.*, procambium strand; *A–B*, see text; *C–D*, see text.

Plate 25

Fig. 3. Photograph (×336) of median longitudinal section showing older leaf primordium. *PRO.*, procambium; *A.M. of L.*, apical meristem of leaf; *AD.T.*, adaxial tissue; *AB.T.*, abaxial tissue; *VAC.*, vacuolation; *AX.B.F.*, axillary bud primordium.

Fig. 4. Photograph (×336) of oblique longitudinal section showing still older leaf primordium. *P.S.*, procambium strand; *L. of V.*, limit of vacuolation; *S.L.*, surface layer of cells of leaf primordium with dense protoplasmic contents.